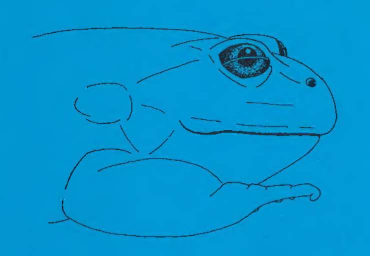
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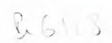
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Deux nouvelles espèces du genre *Telmatobius* (Anura: Leptodactylidae) en provenance de El Moreno (Province de Jujuy, Argentine)

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Two new species of *Telmatobius* (Anura: Leptodactylidae) are described, based on specimens from El Moreno, Jujuy, Argentina. For the first time, two species of this genus are recorded living in sympatry in Argentina.

En 1901, l'expédition suédoise d'Earland NORDENSKIÖLD a recueilli une série de *Telmatobius* qui fut ultérieurement rapportée par ANDERSSON (1906) à *Telmatobius jeslkii* (Peters). Cependant, cette espèce n'a jamais été signalée ailleurs qu'au Pérou, ce qui incita BARBOUR & NOBLE (1920) à mettre en doute l'identification d'ANDERSSON et à attribuer, à titre d'hypothèse, ce matériel à *Telmatobius hauthali* Koslowsky, 1895. GALLARDO (1962) se rangea à l'opinion de BARBOUR & NOBLE, mais rien n'a été fait pour résoudre réellement le problème.

En février 1987, l'un de nous a pu refaire en partie l'itinéraire de l'expédition suédoise grâce à la carte publiée par son archéologue (VON ROSEN, 1957) et pu localiser le village appelé El Moreno (23° 52'S 65° 48'W). Grande fut notre surprise de trouver dans la région deux espèces, ce qui constitue le premier cas de sympatrie connu pour le genre en Argentine. Toutes deux sont nouvelles et décrites ci-après.

Nous n'avons pu localiser la Stockholm Hogskola, lieu où fut déposé le matériel examiné par ANDERSSON et il nous est donc impossible de dire à quelle espèce ou quelles espèces il appartient.



Fig. 1. – *Telmatobius platycephalus* (FML 03763), vue latérale de la tête.

Telmatobius platycephalus sp. nov.
(fig. 1-7)

Holotype. – FML 03763, femelle adulte. El Angosto, 6 km S de El Moreno, Province de Jujuy, Argentine, 3600 m. 12/II/87. Col. E. Lavilla, A. Marcus, R. Montero.

Etymologie du nom spécifique. – De πλατύς, aplati et χεφαλη, tête.

Diagnose. – Diffère par la structure de la peau dorsale des autres espèces argentines, celle-ci étant complètement lisse chez *T. stephani* et *T. ceiorum*, complètement verruqueuse chez *T. marmoratus*, *T. atacamensis* et *T. oxycephalus*, complètement épineuse chez *T. scrocchii*, *T. laticeps* et *T. pisanoi*, pourvue de rares épines et verrues dispersées chez *T. schreiteri*, et ayant un aspect poreux chex *T. contrerasi*. De *T. hauthali* il diffère par l'absence des glandes post-oculaires chez la femelle.

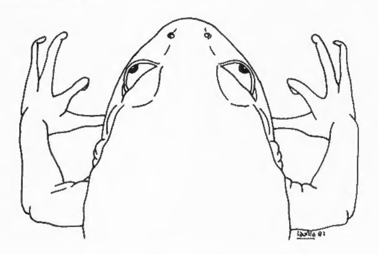


Fig. 2. – *Telmatobius platycephalus*, vue dorsale de la tête.

Longueur totale (SVL) : 61 mm. Tête déprimée, à région gulaire plate, plus longue (21,8 mm) que large (20,9 mm). Indice céphalique : 0,96. Largeur de la tête environ 2,9 fois et longueur 2,8 fois dans la longueur du corps (distance museau-anus).

Museau quelque peu arrondi à légèrement pointu en vue dorsale, arrondi en vue latérale, plus court que le diamètre oculaire (distance narine-bout du museau/diamètre de l'œil : 0,79). Canthus rostralis arrondi, peu différencié et région loréale concave. Lèvre non glandulaire, mince, plus saillante antérieurement. Pupille ronde, membrane nictitante transparente, ornée d'une mince bande pigmentée sur son rebord libre ; diamètre de l'œil (5,2 mm) supérieur à la distance œil-narine (4 mm) ; distance entre les angles antérieurs des yeux environ 2,6 fois dans la largeur de la tête. Pli supratympanique mince, non glandulaire et légèrement oblique, s'étendant depuis l'angle postérieur de l'œil jusqu'à la région médio-dorsale de la glande postcommissurale, au-dessus et en avant de la base du membre antérieur. Glande postcommissurale subcirculaire, saillante, avec pustules peu visibles et sans excroissances cornées. Tympan et anneau tympanique invisibles ; pli suprahuméral absent. Orifices nasaux circulaires, non saillants, à bords légèrement en relief, dirigés dorsalement et situés environ à mi-distance de l'œil et du bout du museau. Distance internasale (3,8 mm) inférieure à la distance naso-oculaire (4 mm) et 1,2 fois inférieure à la distance interoculaire. Langue ronde, non échancrée et libre en arrière. Dents prémaxillaires et maxillaires aigües et minces ; dents vomériennes présentes ; choanes ovales.

Région dorsale de la tête et région centrale du dos lisses ; périphérie et partie postérieure de la région dorsale du corps parsemées de pustules basses, petites, abondantes et sans excroissances cornées ; flancs et région ventrale du corps lisses ; plis gulaire et thoracique absents. Région postérieure des cuisses avec pustules similaires à celles du dos ; le reste lisse. Plis glandulaires latéraux absents. Ouverture cloacale postéro-dorsale, au niveau de la région médio-dorsale des cuisses. Pli cloacal petit et festonné, n'arrivant pas à couvrir l'ouverture. Pli supracloacal glandulaire et bien apparent ; région péricloacale plissée avec quelques pustules.

Doigts arrondis et non dilatés au bout. Tubercule métacarpal interne elliptique et non saillant, 1,6 fois plus long que le tubercule métacarpal externe qui est ovale et aplati. Tubercules sous-articulaires hémisphériques, saillants et entiers, de formule I(1), II(1), III(2), IV(2). Palmure réduite à un pli cutané vestigial sur le bord interne des 2ème et 3ème doigts. Paume avec granulations de taille variable. Longueur relative des doigts du plus long au plus court : 3 – 4 – 1 – 2.

Orteils arrondis et non dilatés au bout, les 4ème et 5ème légèrement plus étroits distalement. Tubercule métatarsal interne elliptique et saillant ; tubercule métatarsal externe petit, conique, également saillant. Tubercules sous-articulaires hémisphériques, entiers et saillants, selon formule I(1), II(1), III(2), IV(3), V(2). Plantes pourvues de nombreux granules petits et bas. Plis tarsal et métatarsal présents, allant de la moitié du tarse au bout du 1er orteil. Formule de la palmure : I(1), II(2-1/2), III(2-1), IV(2-1), V(1/3). Relation entre la longueur du pied et la taille (SVL) : 0,43. Talons non en contact quand les cuisses sont à angle droit avec le corps. Articulation tibio-tarsale atteignant le coin de la bouche quand la patte est étendue vers l'avant. Tibia 2,9 fois plus long que large, représentant 40 % de la taille.

Tableau I. – *Telmatobius platycephalus*, mesures des paratypes.

MA : longueur du corps ; LT : longueur de la tête ; IT : largeur de la tête ; NM : narine – bout du museau ; NO : narine – œil ; DN : distance internasale ; DO : distance entre les bords antérieurs des yeux ; Tmc : tubercule métacarpal ; Tce : tubercule carpal externe ; Tmi : tubercule métatarsal interne ; Tme : tubercule métatarsal externe ; O : diamètre oculaire ; TB : longueur du tibia ; ITB : largeur du tibia ; PD : longueur du pied (depuis le bord postérieur).

	03769	03765	03790
MA	60.0	56.0	50.0
LT	22.0	20.4	17.8
IT	21.2	19.6	16.7
NM	4.4	4.4	4.2
NO	3.8	3.9	3.9
DN	3.7	3.7	2.96
DO	8.1	8.2	6.7
Tmc	3.9	3.7	3.3
Tce	2.89	2.65	2.54
Tmi	2.80	2.78	2.02
Tme	1.44	1.38	1.40
O	4.9	4.5	4.4
TB	25.1	25.1	21.1
ITB	8.3	6.7	7.0
Pd	26.8	25.7	21.5

Coloration. – Dos gris verdâtre (gris moyen dans l'alcool) avec petites taches plus sombres, de forme irrégulière et distribuées au hasard, anastomosées dans la région centrale du dos et formant des taches plus grandes. Ventre de couleur crème, avec zones jaunes sous les pattes et de petites taches grises irrégulières dans la région axillaire.

Allotype. – FML 03764. Mâle adulte. San José de Chañi, versant occidental du Massif du Chañi, entre El Moreno et Abra de Palomar, Prov. Jujuy, Argentine, 3750 m. 13/II/87. Coll. E. Lavilla, A. Marcus, R. Montero.

On signale ici seulement les différences avec l'holotype. Longueur totale 54 mm. Indice céphalique : 0,98. Distance narine-bout du museau : 93 % du diamètre oculaire. Distance entre les coins antérieurs des yeux ± 2,6 fois dans la largeur de la tête. Glande post-commissurale avec excroissances cornées.

Texture de la peau semblable à celle de l'holotype, mais verrues pourvues chacune d'une pointe de kératine. D'une aisselle à l'autre, une bande couverte de minuscules épines cornées. Un pli gulaire.

Tubercule métacarpal interne 1,74 fois plus long que l'externe. Pouce pourvu d'épines nuptiales petites et nombreuses formant une plaque à peu près continue. Longueur du pied sur la longueur du corps (SVL) : 0,45. Tibia 2,8 fois plus long que large, représentant 42 % de la longueur du corps.

Autres paratypes. – FML 03769, El Angosto, Jujuy, Argentine, 12/II/87, Lavilla – Marcus – Montero col. ; FML 03790, San José de Chañi, Jujuy, Argentine, 13/II/87, Lavilla – Marcus – Montero col.; FML 03765, El Moreno, Jujuy, Argentine, 11/II/87, Lavilla – Montero – Marcus col.

Les caractères sexuels sont confirmés par les paratypes. Voir variation dans le Tableau I.

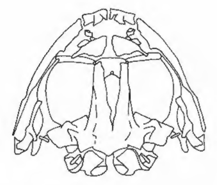


Fig. 3. – *Telmatobius platycephalus*, vue dorsale du crâne.

Ostéologie (fig. 3 à 7). – Caractérisation préliminaire, basée sur le squelette d'une seule femelle (FML 04371) provenant d'El Moreno, Jujuy, Argentine. Préparation du squelette selon WASSERSUG (1976).

Crâne (fig. 3). – Fronto-pariétaux soudés en arrière, séparés en avant par une fontanelle en forme de V, donnant l'impression d'un seul fronto-pariétal bifide. Portion frontale couvrant les bords du sphénethmoïde sur toute leur longueur, laissant à découvert la région médiane. En arrière, fronto-pariétal soudé aux prootiques mais non aux exoccipitaux, n'atteignant pas le foramen magnum, non en contact avec le squamosal ni avec les nasaux. Nasaux subtriangulaires, transversalement orientés, à bords irréguliers, proches l'un de l'autre et en contact avec le sphénethmoïde, leur processus maxillaire n'atteignant pas la pars facialis du maxillaire. Prémaxillaires non soudés entre eux, ni avec les maxillaires. Processus laminaires irréguliers, obliques et convergents. Pars dentalis portant 4 à 6 dents. Pars palatina avec un processus maxillaire court. Maxillaires très longs, les trois quarts antérieurs portant de 24 à 26 dents. Pars palatina laminaire étroite, réduite le long de la portion édentée de l'os. Pars facialis avec processus préorbital bien développé, mais sans processus postorbital. Au-

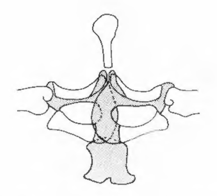


Fig. 4. – *Telmatobius platycephalus*, ceinture scapulaire (surface en pointillé = cartilage).

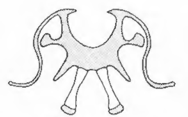


Fig. 5. – *Telmatobius platycephalus*, hyoïde (surface en pointillé = cartilage).

cun contact avec la branche zygomatique du squamosal ni avec le ptérygoïde. Quadrato-jugal court et arrondi, en étroit contact avec le squamosal, non superposé au maxillaire ; carré non ossifié (fig. 7). Parasphénoïde à processus cultriforme long, dépassant de peu l'extrémité antérieure du sphénethmoïde, non en contact avec les palatins (fig. 6). Ailes plus courtes que le processus cultriforme, couvrant quasi complètement les capsules otiques, et très légèrement le bord antérieur des exoccipitaux. Prévomers non en contact avec un autre os. Aile antérieure nettement plus grande que l'aile postérieure. Processus odontophore à peu près perpendiculaire à l'axe antéro-postérieur, muni de 3 ou 4 dents. Palatins en forme de baguette mince, un peu élargie à son extrémité latérale, perpendiculaires à l'axe longitudinal, séparés du sphénethmoide. Septomaxillaires bien développés, situés un peu au-dessous du processus dorsal des prévomers. Extrémité antérieure du ptérygoïde superposée à l'extrémité latérale du palatin. Branche postérieure plus longue que la branche médiale, celle-ci non en contact avec les prootiques mais superposée à eux. Branche postérieure séparée du complexe formé par le quadrato-jugal et le squamosal. Branches antérieure et postérieure longues, sigmoïdes. Squamosal à branche otique très courte, n'atteignant pas les prootiques ; branche inférieure en étroit contact avec le quadrato-jugal, plus longue que le processus zygomatique, celui-ci aplati. Sphénethmoïde court (environ 1/3 de la longueur de l'orbite), continu dorsalement, mais incomplet ventralement, le vide étant cependant couvert par le processus cultriforme du parasphénoïde. Septum internasal non ossifié. Exoccipitaux séparés des prootiques, ceux-ci séparés l'un de l'autre et sans ornementation dorsale. Condyles occipitaux semilunaires. Columelle ossifiée.

Ceinture scapulaire (fig. 4). – Arcifère. Omosternum cartilagineux ; clavicules ar-

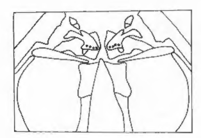


Fig. 6. – *Telmatobius platycephalus*, détail de la région du sphénethmoide, en vue ventrale.

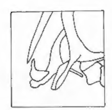


Fig. 7. – *Telmatobius platycephalus*, détail de la région du quadrato-jugal, en vue ventrale.

quées, non soudées à l'omoplate et séparées des coracoïdes par un cartilage légèrement calcifié. Omoplate à pars acromialis plus large que la pars glenoidalis, celle-ci bicipitale, séparée de la suprascapula par une bande cartilagineuse bien visible. Cleithrum bifurqué dorsalement, la branche antérieure la plus longue. Epicoracoïdes cartilagineux. Métasternum constitué d'une plaque large et carrée à côtés concaves, et partie distale fendue.

Main. – Cubital et radial libres, le dernier plus grand. Central proximal libre, presqu'aussi grand que le radial. Carpiens externes (3ème, 4ème et 5ème) soudés au 2ème central. 2ème carpien libre s'articulant avec les deux centraux et le 2ème métacarpien. Prépollex de 5 phalanges, la dernière la plus petite. Tous ces éléments sont cartilagineux, mais présentent des centres d'ossification.

Pied. – Tibial et péronéal unis par un cartilage commun, minéralisé proximalement et distalement. Trois premiers tarsiens libres et cartilagineux. Préhallux de 4 phalanges, cartilagineux.

Hyoïde (voir fig. 5). – Processus antéromédiaux bien développés et thyrohyaux bien séparés.

Telmatobius hypselocephalus sp. nov.
(fig. 8-14)

Holotype. – FML 03768, femelle adulte. El Angosto, 6 km S de El Moreno, Jujuy, Argentina. 3600 m. 12/II/1987. Coll. E. LAVILLA, A. MARCUS, R. MONTERO.

Etymologie du nom spécifique. – De υψηλος, haut et χεφαλη, tête.

Diagnose. – Diffère de *T. platycephalus* par le profil globuleux de la tête, et des autres espèces argentines par la présence d'épines et pustules cornées limitées aux flancs et la région postérieure du dos.

Longueur totale (SVL) : 62 mm. Tête haute, à région gulaire convexe, un peu plus large (20,7 mm) que longue (20,2 mm). Indice céphalique : 1,02. Largeur de la tête environ 2,9 fois et longueur à peu près 3,1 fois dans la longueur totale.

Museau arrondi en vues dorsale et latérale, plus court que le diamètre oculaire (distance narine-bout du museau/diamètre de l'œil : 0,83). Canthus rostralis arrondi, peu distinct, et région frénale concave. Lèvres non glandulaires, minces et uniformément saillantes. Pupille ronde. Membrane nictitante transparente, ornée d'une bande pigmentée sur son bord libre ; diamètre oculaire (5,2) supérieur à la distance oculo-nasale (2,93) ; distance entre les coins antérieurs des yeux environ 2,7 fois dans la largeur de la tête. Pli supratympanique

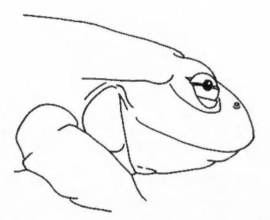


Fig. 8. – *Telmatobius hypselocephalus* (FML 03768), vue latérale de la tête.

mince, glandulaire et légèrement oblique, s'étendant depuis le coin postérieur de l'œil jusqu'à la base du membre antérieur, au-dessus et devant. Glande postcommissurale peu développée, non saillante, avec quelques verrues portant des excroissances kératinisées. Tympan absent ; anneau tympanique visible, plus à gauche qu'à droite ; pli suprahuméral absent. Orifices nasaux circulaires, à bords légèrement en relief, non saillants, dirigés dorsalement, et situés plus près de l'œil que du bout du museau. Espace internasal (3,7) supérieur à la distance oculo-nasale (2,93), environ la moitié de la distance interoculaire. Langue arrondie, non échancrée, libre en arrière. Dents prémaxillaires et maxillaires minces et acérées, dents vomériennes très réduites ; choanes ovales, transversalement orientées.

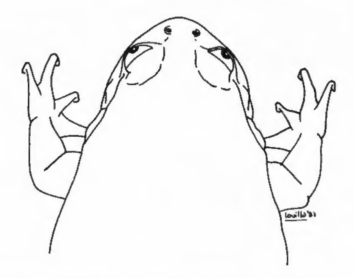


Fig. 9. – *Telmatobius hypselocephalus*, vue dorsale de la tête.

Région centrale de la tête lisse, les paupières granuleuses. Peau dorsale couverte de verrues basses, celles des côtés et de l'arrière avec pustules cornées. Flancs et ventre avec pustules kératinisées plus petites et plus rares. Pli gulaire peu développé ; pli thoracique absent. Partie postérieure et antérodorsale des cuisses pourvue de rares granulations ; le reste lisse. Plis glandulaires latéraux absents.

Ouverture cloacale postérodorsale, au niveau de la région médio-dorsale des cuisses. Pli cloacal petit et festonné, n'arrivant pas à couvrir l'ouverture. Pli supracloacal glandulaire et bien visible. Région péricloacale plissée, verruqueuse.

Doigts arrondis au bout, non dilatés. Tubercule métacarpal interne elliptique et non saillant, 1,6 fois plus long que le tubercule métacarpal externe, celui-ci ovale et aplati. Tubercules sous-articulaires hémisphériques, entiers et saillants selon formule I(1), II(1), III(2), IV(2). Palmure réduite à un pli vestigial sur le bord interne des 2ème et 3ème doigts. Paume couverte de granulations hémisphériques, petites et saillantes. Longueur relative des doigts du plus long au plus court : 3 - 4 - 1 - 2.

Orteils arrondis au bout, non dilatés, les 4ème et 5ème légèrement plus étroits distalement. Tubercule métatarsal interne elliptique et aplati. Tubercule métatarsal externe petit, hémisphérique et saillant. Tubercules sous-articulaires hémisphériques, saillants, non divisés, selon formule I(1), II(1), III(2), IV(3), V(2). Plante avec quelques granulations petites et basses. Plis métatarsal et tarsal présents, allant du bout du 1er orteil à la moitié du tarse. Formule de la palmure I(1), II(2-1), III(2-1 3/4), IV(3 1/4-3), V(1). Pied environ 40 % de la longueur du corps. Tibia 2,9 fois plus long que large, représentant 40 % de la taille.

Coloration. – Dorsalement brun verdâtre sombre, uniforme ; ventralement verdâtre clair, avec quelques taches orangées dans la région fémorale, brun grisâtre en alcool.

Allotype. – FML 03767, mâle adulte. El Angosto, 6 km S de El Moreno, Jujuy, Argentina. 3600 m. 12/II/87. Coll. E. LAVILLA, A. MARCUS, R. MONTERO.

Diffère de l'holotype par les traits suivants:

Longueur totale 60 mm. Tête plus longue (21,5 mm) que large (20,8 mm). Indice céphalique 0,97. Distance narine-bout du museau/diamètre oculaire 0,70. Distance entre les coins antérieurs des yeux environ 2,7 fois dans la largeur de la tête. Glande postcommissurale développée. Anneau tympanique non visible.

Verrues dorsales peu développées, mais excroissances cornées présentes. Flancs et ventre lisses avec de minuscules épines cornées dispersées dans la région pectorale. Pli supracloacal peu marqué et région péricloacale sans glandes. Tubercule métacarpal interne 1,12 fois plus long que l'externe. Epines nuptiales du pouce petites, très nombreuses et denses. Talon atteignant la commissure, quand la patte postérieure est étendue en avant. Longueur du pied sur la longueur du corps 0,41. Tibia 3,0 fois plus long que large, représentant 40 % de la longueur totale.

Autres paratypes. – FML 03766/D, 03766/E, 03766/F, 03766/G, 03766/H et 03766/J, El Moreno, Jujuy, Argentine, 13/II/87, LAVILLA – MARCUS – MONTERO col.

Les caractères sexuels sont confirmés par les paratypes. Voir variation dans le Tableau II.

Tableau II. – *Telmatobius hypselocephalus*, mesures des paratypes.

MA . longueur du corps ; LT : longueur de la tête ; IT : largeur de la tête ; NM : narine – bout du museau ; NO : narine – œil ; DN : distance internasale ; DO : distance entre les bords antérieurs des yeux ; Tmc : tubercule métacarpal ; Tce · tubercule carpal externe ; Tmi : tubercule métatarsal interne ; Tme : tubercule métatarsal externe ; O : diamètre oculaire ; TB : longueur du tibia ; ITB · largeur du tibia ; PD : longueur du pied (depuis le bord postérieur).

	03766D	03766E	03766F	03766G	03766H	03766J
MA	55.0	50.0	68.0	60.0	59.0	58.0
LT	18.2	17.4	23.0	19.7	19.7	17.7
IT	17.9	16.8	26.2	20.0	20.0	18.3
NM	4.5	3.9	5.0	4.0	4.0	3.8
NO	3.1	3.1	3.8	2.73	2.95	2.70
DN	2.94	3.0	4.4	3.6	4.2	3.4
DO	7.4	7.2	9.2	7.8	7.7	7.0
Tmc	2.82	3.0	4.5	3.5	2.61	2.86
Tce	2.68	2.80	2.43	2.49	2.65	2.04
Tmi	2.53	2.45	2.70	2.48	2.52	2.12
Tme	1.44	1.40	1.10	1.53	1.40	1.23
O	4.6	4.9	6.7	5.4	5.1	5.9
TB	22.7	22.0	29.4	24.1	22.4	22.1
ITB	8.0	8.1	9.2	9.0	8.9	7.9
PD	23.9	22.8	28.4	25.6	24.2	23.3

Ostéologie (fig. 10 à 14). – Comme on n'a préparé qu'un seul squelette de cette espèce (femelle adulte, FML 04372) ainsi que de la première, la caractérisation ostéologique reste préliminaire et on notera seulement les différences avec *Telmatobius platycephalus*. Squelette préparé selon Wassersug, 1976.

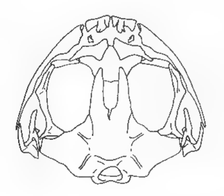


Fig. 10. – *Telmatobius hypselocephalus*, vue dorsale du crâne.

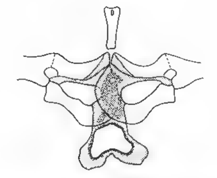


Fig. 11. – *Telmatobius hypselocephalus*, ceinture scapulaire (surface en pointillé – cartilage).

Crâne (fig. 10). – Fontanelle fronto-pariétale en forme de U et non de V, moins large. Portion frontale couvrant seulement la base du sphénethmoïde, celui-ci presque complètement exposé. En arrière, fronto-pariétaux soudés aux exoccipitaux et aux prootiques. Nasaux subquadrangulaires, à bords internes convexes, les autres concaves, proches l'un de l'autre, recouvrant largement le sphénethmoïde. Prémaxillaires portant de 5 à 7 dents. Maxillaires portant environ 20 dents, en contact avec l'extrémité antérieure du ptérygoïde. Quadrato-jugal long et pointu, en étroit contact avec le squamosal, son quart antérieur longeant le maxillaire. Processus cultriforme du parasphénoïde couvrant à peu près les deux tiers du sphénethmoïde. Prévomers à processus odontophore portant une seule dent ; son aile postérieure fortement réduite. Palatins en contact avec les maxillaires, leur tiers interne recouvrant le sphénethmoïde. Carré ossifié ; ptérygoïde, carré, quadrato-jugal et squamosal en contact (fig. 14). Branche otique du squamosal en contact avec le prootique et plus courte que la branche inférieure. Sphénethmoïde fort développé, formant une structure continue aussi bien dorsalement que ventralement ; partie antérieure en forme de prisme trapézoïdal, atteignant les choanes (fig. 13). Côtés du chondrocrâne ossifiés. Exoccipitaux soudés aux prootiques, ornementés.

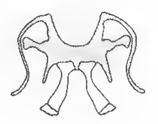


Fig. 12. – *Telmatobius hypselocephalus*, hyoïde (surface en pointillé – cartilage).

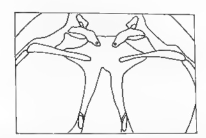


Fig. 13. – *Telmatobius hypselocephalus*, détail de la région du sphénethmoïde en vue ventrale.

Ceinture scapulaire (fig. 11). – Clavicules soudées à l'omoplate et séparées des coracoïdes par un cartilage calcifié. Pars acromialis et pars glenoidalis de l'omoplate subégales. Omoplate séparée de la suprascapula par une étroite bande de cartilage. Cleithrum bifurqué, les deux branches à peu près égales. Epicoracoïdes largement calcifiés. Métasternum trapézoïdal, fendu à la base, fortement calcifié.

Main. – Diffère seulement de celle de *Telmatobius platycephalus* par son ossification complète et la présence d'un os sésamoïde elliptique entre le radius et le radial.

Pied. – Diffère seulement de celui de *Telmatobius platycephalus* par son ossification presque complète (seules les 3 phalanges distales du préhallux restent cartilagineuses), le tibial et le péronéal soudés à leurs extrémités.

Hyoïde (fig. 12). – Processus antéro-médiaux absents et thyrohyaux rapprochés.



Fig. 14. – *Telmatobius hypselocephalus*, détail de la région du quadrato-jugal en vue ventrale.

Résumé

Deux nouvelles espèces du genre *Telmatobius* (Anura : Leptodactylidae) sont décrites d'après un matériel provenant de El Moreno, Jujuy, Argentine. Ceci revêt un intérêt particulier car c'est la première fois qu'on observe deux espèces de ce genre vivant en sympatrie en Argentine.

RÉFÉRENCES BIBLIOGRAPHIQUES

ANDERSSON, L.G., 1906. – On batrachians from Bolivia, Argentina and Peru, collected by Erland Nordenskiöld, 1901-1902, and Nils Holmgren, 1904-1905. *Arkiv. f. Zool.*, **3** (12) : 1-19, 1 pl.

BARBOUR, T. & NOBLE, G.K., 1920. – Some amphibians from northwestern Peru, with a revision of the genera *Phyllobates* and *Telmatobius*. *Bull. Mus. Comp. Zool.*, **63** (8) : 395-427, 3 pl.

GALLARDO, J.M., 1962. – Los géneros *Telmatobius* y *Batrachophrynus* en la Argentina (Anura : Leptodactylidae). *Neotropica*, **8** (26) : 45-58.

VON ROSEN, E., 1957. – Un mundo que se va. *Opera Lilloana*, **1** : i – xxiii + 1-307, 45 pl.

WASSERSUG, R.J., 1976. – A procedure for differential staining of cartilage and bone in whole formalin fixed vertebrates. *Stain Tech.*, **51** : 131-134.

Alytes, 1988, 7 (3): 90-96.

A new species of *Telmatobius* (Anura : Leptodactylidae) from Catamarca (Argentina)

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A new species of *Telmatobius*, *T. pinguiculus*, is described from the mountains of Catamarca Province, Argentina. A preliminary key to the species of *Telmatobius* from this province is given.

Introduction

As currently understood, the Argentinian fauna of *Telmatobius* consists of 13 species, four of which are reported from Catamarca Province. All of them are stream dwellers and have restricted, not overlapping ranges : *Telmatobius hauthali* is found in one thermal spring at Aguas Calientes (27° 14'S 68° 16'W), *T. scrocchii* at Campo El Arenal (27° 06'S 66° 20'W), *T. stephani* in the isolated mountain range of El Manchao (28° 08'S 65° 54'W) and *T. ceiorum* in the forested areas of Nevados del Anconquija (27° 08'S 66° 02'W).

Field work in the mountains of this province has continued to reveal undescribed species of frogs and lizards, including the one herein described from La Cienaga (about 27° 30'S 67° 00'W), near Medanitos (27° 32'S 67° 36'W).

Specimens used for descriptions are housed at Fundación Miguel Lillo Collections (FML).

Telmatobius pinguiculus n.sp.
(fig. 1-8)

Holotype. – FML 03910. Adult female.

Etymology of the specific name. – This name is a diminutive of the Latin word *pinguis*, meaning somewhat fat.

Diagnosis. – Done in relation with the other species of *Telmatobius* inhabiting Catamarca province. Spiny skin of *T. pinguiculus* sets the difference with *T. hauthali* (granular), *T. ceiorum* and *T. stephani* (smooth). The absence of suprahumeral fold and the presence of postcommissural gland in *T. pinguiculus* set the differences with *T. scrocchii*, which has the opposite condition in both characters.

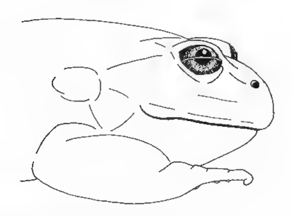


Fig. 1. – *Telmatobius pinguiculus*, lateral view of the holotype.

Description. – Snout-vent length (SVL) 56.0 mm. Head wider (18.6) than long (16.1) ; cephalic index 1.15. Head width about three times, and head length about 3.5 times in SVL.

Snout rounded in dorsal and lateral view, and shorter than eye diameter (snout length/eye diameter : 0.66). Canthus rostralis indistinct and rounded ; loreal region nearly flat and inclined laterally. Pupil circular and palpebral membrane pigmented only in a narrow strip in the free margin ; interocular distance about 2.3 times in head width. Tympanum and tympanic ring indistinct ; supratympanic fold rather glandular, with small corneal projections, running from posterior corner of eye to the dorsal border of post-commissural gland. Nostrils rounded, flanged and not protruding, without projections or inflections, directed dorsolaterally and placed closer to eye (3.3) than to tip of snout (3.5) ; internasal dis-

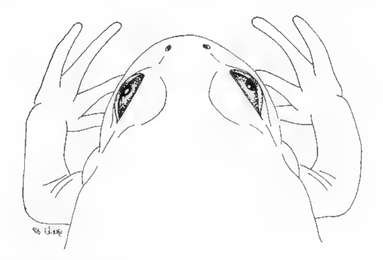


Fig. 2. – Dorsal view of the holotype.

tance (3.1) shorter than naso-ocular distance, and 2.5 times less than interocular distance. Tongue circular. Premaxillary and maxillary teeth small and sharp ; vomerine teeth present.

Skin on back and limbs with flat warts and small corneal spines ; ventrally smooth, with few corneal spines on borders. Cloacal opening at about mid-level of thighs ; anal fold small, not covering the cloaca.

Body moderately stout. Tip of fingers rounded and not expanded. Outer metacarpal tubercle almost quadrangular, about the same size (3.2) as the inner, elliptical, metacarpal tubercle (3.3) ; latter in contact with a round, flat, palmar tubercle, forming a heart-shaped structure. Subarticular tubercles hemispherical, protruded and not divided ; number of tubercles on each digit follows the formula I(1) – II(1) – III(2) – IV(2), the one on the pollex being the greatest. Palmar tubercles present. Webbing absent ; no dermal folds on fingers. Relative length of digits, from longer to shorter : 3>4>1>2.

Tibio-tarsal articulation reaching the forearm ; heels in contact when femurs bent at right angle to body. Low fold from the tip of hallux to tibio-tarsal joint. Inner metatarsal tubercle elliptical and slightly protruding, larger (2.72) than the rounded, outer metatarsal tubercle (1.52). Subarticular tubercles hemispherical, protruding and not divided ; number of tubercles on each digit follows the formula I(1) – II(2) – III(2) – IV(3) – V(2). A single palmar tubercle at the base of each toe ; supernumerary tubercles on toes III, IV and V. Tip of toes rounded. Relative length of digits, from longer to shorter 4>5>3>2>1. Palmar formula : I(1) ; II(2 – 1) ; III(2 – 2) ; IV(3 – 3) ; V(1). Plantar surface spiny. Ratio of foot length/SVL : 0.46. Tibia 3.3 times longer than wide, 46% of SVL.

Coloration (in alcohol). – Dorsally dark brownish-gray, with small, darker spots scattered ; ventrally pale gray.

Allotype. – FML 03920. Adult male. The same data as for the holotype.

Only the main differences with the holotype are pointed out.

SVL 53.0 mm. Head longer (17.3) than wide (16.2) ; cephalic index 0.93. Head width about 3.3 times, and head length about 3.1 times in SVL.

Snout shorter than eye diameter (snout length/eye diameter : 0.72), and interocular distance about 2.2 times in head width. Nostrils placed closer to eye (3.0) than to tip of snout (3.6) ; internasal distance (2.94) slightly shorter than naso-ocular distance (3.0) and about 2.4 times less than interocular distance.

Body slenderer, with a greater number of horny spines on chest. Inner metacarpal tubercle (3.0) about the same size as the outer (2.94), and not in contact with single plantar tubercle. Nuptial pad on the inner surface of pollex, consisting of a slightly cornified plate with numerous, strong, conical spines.

Forelimbs proportionally longer ; tibio-tarsal articulation reaching the posterior corner of eye ; tarsal fold shorter and more evident, reaching the distal 1/3 of tarsus ; supernumerary tubercles only on the fifth toe. Palmar formula : I(1) ; II(2 – 1) ; III[(2 – 1) (2 – 1 3/4)] ; IV(3 – 2) ; V(1). Ratio of length of foot/SVL 0.41. Tibia 3.1 times longer than wide, representing 44.5% of SVL.

Table I. – Measurements (in millimeters) of holotype, allotype and other paratypes of *Telmatobius pinguiculus*.

H : holotype ; A . allotype ; 1 to 7 : other paratypes ; SVL : snout-vent length ; HL : head length ; HW : head width ; SL : snout length (from anterior border of nostril to tip of snout) ; NO : naso-ocular distance (from posterior border of nostril to anterior border of eye) ; IN : internasal distance ; IO : interocular distance ; IMT : inner metacarpal tubercle ; OMT : outer metacarpal tubercle ; Imt · inner metatarsal tubercle ; Omt · outer metatarsal tubercle ; E : eye diameter ; T . tibia length ; t : tibia width ; F : foot length.

	H	A	1	2	3	4	5	6	7
SVL	56.0	53.0	50.0	55.0	52.0	51.0	51.0	53.0	50.0
HL	16.1	17.3	17.0	17.4	14.5	16.0	16.3	15.6	16.8
HW	18.6	16.2	16.7	17.0	15.6	16.2	16.8	18.1	16.3
SL	3.5	3.6	3.1	3.5	3.1	3.8	3.8	3.6	3.3
NO	3.3	3.0	3.2	2.39	2.78	3.2	3.4	3.4	2.92
IN	3.1	2.94	2.78	3.3	2.69	2.63	3.2	3.1	2.95
IO	7.9	7.2	7.3	7.1	7.2	7.3	7.8	8.3	7.2
IMT	3.3	3.0	2.80	2.87	2.76	2.82	2.93	3.6	3.2
OMT	3.2	2.94	2.61	2.56	2.52	2.72	2.55	3.0	2.56
Imt	2.72	2.21	2.34	2.65	2.35	2.46	2.68	2.48	2.25
Omt	1.52	0.74	1.30	1.08	1.20	1.24	1.26	1.24	1.02
E	5.3	5.0	5.1	5.4	4.9	5.5	4.4	4.3	4.8
T	23.6	23.6	22.7	23.9	22.9	22.6	22.8	24.1	21.3
t	7.1	7.7	7.2	6.7	7.2	7.2	7.9	8.0	7.4
F	26.0	25.3	24.2	26.4	25.0	24.1	27.0	23.0	23.0

Other paratypes. – FML 03921/1 to 5, adult females ; FML 03921/6 and 7, adult males ; the same data as for the holotype.

The sexual characters and degree of morphological variation between the holotype and allotype are confirmed by the paratypes. See variation in measurements in Table I.

Osteology (fig. 3 to 8). – The following description, based on only one adult female (FML 04373), is considered preliminary. General features of the skeleton are designed in fig. 3 to

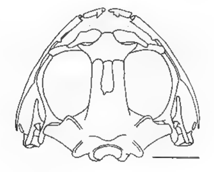


Fig. 3. – General view of skull (scale = 5 mm).

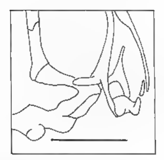


Fig. 4. – Detail of quadratojugal area (scale = 5 mm).

8, and only the most noticeable characters are noted. Skeleton for study was prepared following WASSERSUG's (1976) technique.

Skull. – Frontoparietal a single bone, with frontal region bifurcated. Premaxillary, maxillary and prevomer toothed. Palatines in contact with pterygoid and sphenethmoid ; the latter, as a complete ring, expanded anteriorly and laterally, with a wing-like process at each side. Ventrally, the sphenethmoid projecting posteriorly at about 1/3 the length of cultriform process of parasphenoid.

Pterygoid and squamosal in close contact with a strong quadratojugal ; pars articularis of quadrate separated from the jugal projection (this bizarre condition observed bilaterally). Medial ramus of squamosal noticeably short.

Hyoid. – Hyoglossal sinus strong ; anterior process of hyale poorly developed but observable ; alary process and posterolateral process well developed ; posteromedial process ossified, without stalk.

Pectoral girdle. – Omosternum cartilaginous ; sternum bilobed and strongly mineralized ; epicoracoids mineralized. Clavicle fused with scapula ; the latter firmly attached to coracoid by means of mineralized tissue.

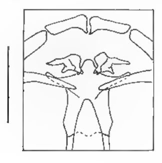


Fig. 5. – Detail of sphenethmoidal region (scale = 5 mm).

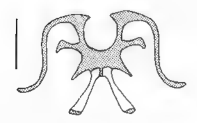


Fig. 6. – Hyoid (stippled area : cartilage ; scale = 5 mm).

Carpus (nomenclature according to ANDERSEN, 1978). – Os centrale postaxiale articulating with metacarpals III, IV and V ; os distal carpale 2 free, articulating with metacarpal II and os centrale postaxiale ; the latter articulating with the basal prepollical element. Ulnare and radiale independent ; an elliptical sesamoid on the radiale. Prepollex with five elements, the distal two cartilaginous.

Tarsus (nomenclature according to ANDERSEN, 1978). – Only three distal tarsal elements present. Os distal tarsale 1 articulating with prehallux ; os distal tarsale 2 articulating with metatarsal II and os distal tarsale 3 articulating with metatarsals III and IV.

PRELIMINARY KEY FOR THE SPECIES OF *TELMATOBIUS* FROM CATAMARCA PROVINCE (ARGENTINA)

1.a. Dorsal skin granular ; postocular protuberances evident ... *T. hauthali* Koslowsky, 1895.
b. Dorsal skin smooth or spiny ; postocular protuberances absent 2

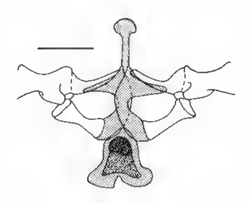


Fig. 7. – Pectoral girdle (stippled area : cartilage ; scale = 5 mm)

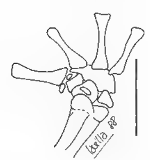


Fig. 8. – Carpus (scale = 5 mm).

2.a. Dorsal skin smooth, with definite, big spots ; ventrally pigmented 3

b. Dorsal skin spiny ; when spots present, usually small and rounded ; ventrally pigmented only on thighs 4

3.a. Tympanum evident ; with round, white edged spots on dorsum and a constant intraocular spot ; ventrally dark gray with yellow, irregular spots scattered .... *T. ceiorum* Laurent, 1970.

b. Tympanum indistinct, with enlarged, dark spots on dorsum ; ventrally gray mottled on belly and thighs .... *T. stephani* Laurent, 1973.

4.a. Suprahumeral fold thick and glandular ; postcommissural gland absent .... *T. scrocchii* Laurent & Lavilla, 1986.

b. Suprahumeral fold absent ; postcommissural gland evident ....*T. pinguiculus* sp. nov.

Résumé

Une nouvelle espèce du genre *Telmatobius* est décrite d'après un matériel provenant de la province de Catamarca, Argentine. Une clef préliminaire des espèces de *Telmatobius* de cette province est donnée.

Literature cited

Andersen, M.L., 1978. – *The comparative myology and osteology of the carpus and tarsus of selected anurans*. Unpubl. PhD Thesis Univ. Kansas : 1 – 235, atlas.

Wassersug, R.J., 1976. – A procedure for differential staining of cartilage and bone in whole formalin fixed vertebrates. *Stain. Tech.*, **51** : 131 – 134.

Leptobrachium parvum Boulenger, 1893 (Amphibia, Anura) : proposed conservation

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The valid name under the Rules of the species now known as *Megophrys parva* (Boulenger, 1893) is in fact *Megophrys monticola* (Günther, 1864) In order to avoid the problems caused by this priority, the International Commission on Zoological Nomenclature is asked to use its plenary powers to place the name *Leptobrachium parvum* Boulenger, 1893 on the *Official List of Specific Names in Zoology*.

Note. — This paper was submitted on 27 May 1981 to the Secretary of the International Commission on Zoological Nomenclature for publication in the *Bulletin of zoological Nomenclature*, but, despite repeated requests since then, has still not been published in this journal. The problem it raised has therefore remained unresolved. This paper is therefore published here as it was submitted, except that a few recent references have been incorporated

(1) The genus *Megophrys* was created by KUHL & VAN HASSELT (1822) for a single species of frogs from Java. In the original description, the name of this species was mentioned twice, but under two different spellings : *montana* (p. 102) and *monticola* (p. 104). During a little more than a century, the name *montana* was universally considered as the valid name of this species, and was the only one to appear in the scientific literature, until the work of SMITH (1931 : 12), where this author suggested to use the name *monticola* for this species. As was shown and discussed in more details elsewhere (DUBOIS, 1982), this action was incorrect, because GRAVENHORST (1829 : 47), acting as first reviser ("first author to have cited together the competing spellings and to have chosen one as the spelling to be used"), had chosen the name *montana*. The name *montana* Kuhl & Van Hasselt, 1822 must therefore be reinstated as the valid name of the type-species by monotypy of *Megophrys* Kuhl & Van Hasselt, 1822. The name "*monticola* Kuhl & Van Hasselt, 1822" must therefore be considered as an incorrect original spelling and, as such, is not an available name. The name *monticola*, which was used for this species by most authors after SMITH's (1931) work, must therefore be considered as an unjustified emendation of *montana* Kuhl & Van Hasselt, 1822, and be credited to SMITH (1931 : 12). (For a more lengthy discussion of this case, see DUBOIS, 1982).

(2) The fact that the name "*monticola* Kuhl & Van Hasselt, 1822" cannot be considered as being available under the Rules has a secondary nomenclatural consequence. GÜNTHER (1864 : 414) created the genus *Xenophrys* for a single new species, which he called *Xenophrys monticola*. BOULENGER (1893 : 344) described this species again, on the basis of new material, under the name *Leptobrachium parvum*. Later, BOULENGER (1908 : 419) considered both names as synonyms and transferred the species to which they both apply into the genus *Me-*

galophrys Wagler, 1830 (an unjustified emendation of *Megophrys* Kuhl & Van Hasselt, 1822). For this species he used the name *parva* Boulenger, 1893, presumably because he considered the name *monticola* Günther, 1864 to be preoccupied in this genus by "*monticola* Kuhl & Van Hasselt, 1822" – although for this latter species he used the correct name *montana* Kuhl & Van Hasselt, 1822! All subsequent authors have admitted both the synonymy of *monticola* Günther, 1864 and *parva* Boulenger, 1893, and the need of using the second of these names for this species, the first one being considered preoccupied in the genus *Megophrys*. Since however, as shown above, the name "*monticola* Kuhl & Van Hasselt, 1822" has no status in nomenclature, the name *monticola* Günther, 1864 is in fact valid, and *monticola* Smith, 1931 (replacement name of *montana* Kuhl & Van Hasselt, 1822) is a junior secondary homonym of this name. It would therefore be necessary to reinstate the name *monticola* Günther, 1864 as the valid name of the species currently known as *Megophrys parva* (Boulenger, 1893). This action would be most inappropriate, for three reasons :

(a) The specific name *monticola* Günther, 1864 has not been in use since its replacement by BOULENGER (1908) by the name *parva* Boulenger, 1893.

(b) The specific name *parva* Boulenger, 1893 has been widely used since then (see e.g. : ANNANDALE, 1908 : 305, 1912 : 29, 1917 : 155 ; HORA, 1922 : 9, 1923 : 582, 1928 : 139 ; NIEDEN, 1923 : 57 ; NOBLE, 1927 : 75 ; BOURRET, 1942 : 203 ; KRIPALANI, 1953 : 60 ; LIU & HU, 1961 : 66 ; DANIEL, 1962 : 667 ; TAYLOR, 1962 : 299 ; GORHAM, 1966 : 21, 1974 : 43 ; INGER, 1966 : 19 ; WALTNER, 1973 : 22 ; DUBOIS, 1974 : 353, 1976 : 12, 1977 : 113, 1980 a : 165, 1980 b : 472, 1981 : 69 ; ANONYMOUS, 1977 : 28 ; FROST, 1985 : 416).

(c) The resurrection of the name *monticola* Günther, 1864 for this species would be liable to create a confusion with the name "*monticola* Kuhl & Van Hasselt, 1822" which, although improperly, has since SMITH's (1931) work been widely used for the species the valid name of which is shown above to be *montana* Kuhl & Van Hasselt, 1822.

(3) Accordingly, I request the International Commission on Zoological Nomenclature :

(1) to use its plenary powers to suppress the specific name *monticola*, as published in the combination *Xenophrys monticola* Gunther, 1864 (: 414), for the purposes of the Law of Priority but not for those of the Law of Homonymy ;

(2) to place the specific name *monticola*, as published in the combinations *Megophrys monticola* Kuhl & Van Hasselt, 1822 (: 104), *Xenophrys monticola* Günther, 1864 (: 414) and *Megophrys monticola* Smith, 1931 (: 12), on the *Official Index of Rejected and Invalid Specific Names in Zoology* ;

(3) to place the specific name *parvum*, as published in the combination *Leptobrachium parvum* Boulenger, 1893 (: 344), on the *Official List of Specific Names in Zoology* ;

(4) to place the specific name *montana*, as published in the combination *Megophrys montana* Kuhl & Van Hasselt, 1822 (: 102) (type-species by monotypy of *Megophrys* Kuhl & Van Hasselt, 1822), on the *Official List of Specific Names in Zoology* ;

(5) to place the generic name *Megophrys* Kuhl & Van Hasselt, 1822 (: 102), type-species, by monotypy, *Megophrys montana* Kuhl & Van Hasselt, 1822, on the *Official List of Generic Names in Zoology*.

RÉSUMÉ

Le nom valide, selon le *Code*, de l'espèce d'Anoures actuellement connue sous le nom de *Megophrys parva* (Boulenger, 1893), s'avère être en fait *Megophrys monticola* (Günther, 1864). De manière à éviter les problèmes pausés par cette priorité, il est demandé à la Commission Internationale de Nomenclature Zoologique de faire usage de ses pleins pouvoirs pour supprimer le nom spécifique *Xenophrys monticola* Günther, 1864 et de placer le nom *Leptobrachium parvum* Boulenger, 1893 sur la *Liste Officielle des Noms Spécifiques en Zoologie*.

LITERATURE CITED

ANONYMOUS, 1977. – [*Systematic keys to the Amphibians of China*]. (In Chinese). Beijing, Kexue Chupanche : [i-iv] + i-v + 1-93, pl. I-XVII.

ANNANDALE, N., 1908. – Notes on some Batrachia recently added to the collection of the Indian Museum. *Rec. Indian Mus.*, **2** : 304-305.

----- 1912. – Zoological results of the Abor expedition 1911-1912. I. Batrachia. *Rec. Indian Mus.*, **8** : 7-36, pl. II-IV.

----- 1917. – Zoological results of a tour in the Far East. Batrachia. *Mem. Asiat Soc. Beng.*, **6** : 119-156, pl. V-VI.

BOULENGER, G.A., 1893. – Concluding report on the Reptiles and Batrachians obtained in Burma by Signor L. Fea, dealing with the collection made in Pegu and the Karin Hills in 1887-88. *Ann Mus. Stor. nat. Genova*, (2a), **13** : 304-347, pl. VII-XII.

----- 1908. – A revision of the oriental pelobatid Batrachians (genus *Megalophrys*). *Proc zool. Soc. Lond.*, **1908** : 407-430, pl. XXII-XXV.

BOURRET, R., 1942. – *Les Batraciens de l'Indochine*. Hanoï, Institut océanographique de l'Indochine : i-x + 1-547, 4 pl.

DANIEL, J.C., 1962. – Notes on some Amphibians of the Darjeeling area, West Bengal. *J. Bombay nat Hist. Soc.*, **59** : 666-668, pl. I-IV.

DUBOIS, A., 1974. – Liste commentée d'Amphibiens récoltés au Népal. *Bull. Mus. natn. Hist. Nat.*, (3), **213** (Zool. 143) : 341-411

----- 1976. – Les grenouilles du sous-genre *Paa* du Népal (famille Ranidae, genre *Rana*). *Cahiers népalais-Documents*, Paris, CNRS, **6** : i-vi + 1-275.

----- 1977. – Chants et écologie chez les Amphibiens du Népal. *In* : *Himalaya. Ecologie-Ethnologie*, Colloques internationaux du CNRS, **268**, Paris, CNRS : 109-118.

----- 1980 a. – L'influence de l'homme sur la répartition des Amphibiens dans l'Himalaya central et occidental. *C.R. Soc. Biogéogr.*, **55** : 155-178.

----- 1980 b. – Notes sur la systématique et la répartition des Amphibiens Anoures de Chine et des régions avoisinantes. IV. Classification générique et subgénérique des Pelobatidae Megophryinae *Bull. Soc. linn. Lyon*, **49** : 469-482.

----- 1981. – Biogéographie des Amphibiens de l'Himalaya : état actuel des connaissances. *In* : *Paléogéographie et biogéographie de l'Himalaya et du sous-continent indien*, Paris, CNRS, *Cahiers népalais* : 63-74.

----- 1982. – Le statut nomenclatural des noms génériques d'Amphibiens créés par Kuhl et Van Hasselt (1822) : *Megophrys*, *Occidozyga* et *Rhacophorus*. *Bull. Mus. natn. Hist. nat.*, (4), **4** (A) . 261-280.

FROST, D.R. (ed.), 1985. – *Amphibian species of the world* Lawrence, Allen Press & Assoc. Syst. Coll. : [i-iv] + i-v + 1-732

GORHAM, S.W., 1966. – Liste der rezenten Amphibien und Reptilien. Ascaphidae, Leiopelmatidea (sic), Pipidae, Discoglossidae, Pelobatidae, Leptodactylidae, Rhinophrynidae. *Das Tierreich*, **85** : i-xvi + 1-222.

----- 1974. – *Checklist of world Amphibians up to January 1, 1970*. Saint-John, The New Brunswick Museum : 1-173.

GRAVENHORST, J.L.C., 1829. – *Deliciae Musei Zoologici Vratislaviensis. Fasciculus primus, continens Chelonios et Batrachiae*. Lipsiae, Sumptibus Leopoldi Vossii . i-xiv + 1-106, pl. I-XVII.

GÜNTHER, A., 1864. – *The Reptiles of British India*. London, Ray Society : i-xxvii + 1-452, pl. I-XXVI.

HORA, S.L., 1922. – Some observations on the oral apparatus of the tadpoles of *Megalophrys parva* Boulenger. *J. & P. Asiat. Soc. Beng.*, (n.s.), **18** : 9-15.

----- 1923. – Observations on the fauna of certain torrential streams in the Khasi Hills. *Rec. Indian Mus.*, **25** : 579-599.

----- 1928. – Further observations on the oral apparatus of the tadpoles of the genus *Megalophrys*. *Rec. Indian Mus.*, **30** : 139-145, pl. III.

INGER, R.F., 1966. – The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana : Zool.*, **52** : 1-402.

KRIPALANI, M., 1953 – On two remarkable tadpoles from the Darjiling distict. *Everyday Sci.*, Hoshiarpur, **2** : 57-61.

KUHL, H. & VAN HASSELT, J.C., 1822. – Uittreksels uit brieven van de Heeren Kuhl en Van Hasselt, aan de Heeren C.J. Temminck, Th Van Swinderen en W. De Haan. *Algemeene Konst- en Letter-Bode*, **7** : 99-104.

LIU, C.-C. & HU, S.-C., 1961 – [*The tailless Amphibians of China*.] (In Chinese). Shanghai : i-xvi + 1-364, pl. I-VI + I-XXVIII.

NIEDEN, F., 1923. – Amphibia. Anura I. Subordo Aglossa und Phaneroglossa, sectio 1 Arcifera. *Das Tierreich*, **46** : i-xxxii + 1-584.

NOBLE, G.K., 1927. – The value of life history data in the study of the evolution of the Amphibia. *Annals N.Y. Acad. Sci.*, **30** : 31-128, pl. IX.

SMITH, M.A., 1931. – The herpetology of Mt. Kinabalu, North Borneo, 13,455 ft. *Bull. Raffles Mus.*, **5** : 3-32, pl. I-II.

TAYLOR, E.H., 1962. – The Amphibian fauna of Thailand. *Univ. Kansas Sci. Bull.*, **63** : 265-599.

WALTNER, R.C., 1973. – Geographical and altitudinal distribution of Amphibians and Reptiles in the Himalayas. Part I. *Cheetal*, **16** : 17-25.

Hyla reinwardtii Schlegel, 1840(?) (Amphibia, Anura) : proposed conservation

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As shown elsewhere in detail (DUBOIS, 1982), the valid name under the Rules of the species now known as *Rhacophorus reinwardtii* [Schlegel, 1840(?)] is in fact *Rhacophorus moschatus* Kuhl & Van Hasselt, 1822. Accordingly, the International Commission on Zoological Nomenclature is asked to use its plenary powers to protect the well-known name *reinwardtii*.

Note. — This paper was submitted on 27 May 1981 to the Secretary of the International Commission on Zoological Nomenclature for publication in the *Bulletin of zoological Nomenclature*, but, despite repeated requests since then, has still not been published in this journal. The problem it raised has therefore remained unresolved, despite other mentions of it in subsequent works (Dubois, 1981 ; Frost, 1985 : 547). This paper is therefore published here as it was submitted, except that a few recent references have been incorporated.

(1) The problem of the validity of the generic name *Rhacophorus* Kuhl & Van Hasselt, 1822 and of the specific names *Rhacophorus reinwardtii* Kuhl & Van Hasselt, 1822 and *Rhacophorus moschatus* Kuhl & Van Hasselt, 1822 has been the matter of several previous discussions (see in particular : Stejneger, 1907, 1925 ; Smith, 1927 ; Wolf, 1936 ; Brongersma, 1942). Recently however, I have presented a new analysis of this case (Dubois, 1982), which solves all problems associated with it, except one, for which an action of the International Commission on Zoological Nomenclature is necessary.

(2) As already recognized by Smith (1927), Wolf (1936) and Brongersma (1942), it is clear that the short diagnosis given by Kuhl & Van Hasselt (1822) for their new genus *Rhacophorus* is sufficient to make this name available as of Kuhl & Van Hasselt (1822) – and not as of Schlegel (1827), as suggested by others (e.g. Stejneger, 1907).

(3) Some authors (e.g. Wolf, 1936 ; Brongersma, 1942 ; Liem, 1970) have suggested that the type-species of *Rhacophorus* was *Hyla reinwardtii* Schlegel, 1840(?) by subsequent designation of Wolf (1936), while others (e.g. Stejneger, 1907 ; Nieden, 1923) have considered that it was *Hyla palmata* Daudin, 1803 by subsequent monotypy in Schlegel (1827). Both these interpretations are incorrect.

(4) When creating their genus *Rhacophorus*, Kuhl & Van Hasselt (1822) associated two specific names with this generic name. The first of these names, *Rhacophorus reinwardtii*, being devoid of any description, definition, or indication, is a nomen nudum and is not available as of Kuhl & Van Hasselt (1822). This specific name became available only with

the publication by SCHLEGEL [1840(?) : pl. 30] of a plate of drawings of a species of frogs which he named *Hyla reinwardtii*. On the other hand, the second specific name proposed by KUHL & VAN HASSELT (1822), *Rhacophorus moschatus*, is accompanied by a very short indication (statement that this species produces a smell of musk) which, although open to some discussion as to its biological relevance (see WOLF, 1936 and BRONGERSMA, 1942), is sufficient, in the meaning of the *Code*, to make the name *moschatus* available as of KUHL & VAN HASSELT (1822). This name being the only available specific name associated with the generic name *Rhacophorus* in the original description of this genus, *Rhacophorus moschatus* Kuhl & Van Hasselt, 1822 is the type-species of *Rhacophorus* Kuhl & Van Hasselt, 1822 by monotypy. Therefore all subsequent designations of type-species for this genus, including the ones mentioned above in (3) and the overlooked designation of *reinwardtii* made by FITZINGER (1843 : 31) are invalid.

(5) A last problem remains to be dealt with. It concerns the status of the name *moschatus*. This name has been considered by all authors until now as a nomen nudum, and consequently has never been used as the valid name of a species. For a long time this name was believed to have been proposed by KUHL & VAN HASSELT (1822) for a species distinct from the one named *reinwardti* by these authors. Several authors (e.g. VAN KAMPEN, 1923 : 254 ; AHL, 1931 : 148 ; WOLF, 1936 : 187) suggested with doubt that this species might be the same which was later called *Hyla margaritifera* by SCHLEGEL (1844 : 107) and even later *Rhacophorus javanus* by BOETTGER (1893 : 338). However, after a detailed inquiry, BRONGERSMA (1942) gave good arguments to support the idea that this name had in fact been proposed for a (probably young) specimen of the species which is now known as *Rhacophorus reinwardtii*. Therefore the names *moschatus* and *reinwardtii* appear to be synonyms. However, since the first one is available as of KUHL & VAN HASSELT (1822) and the second one as of SCHLEGEL [1840(?)], the first one would under the Rules have to replace the second one as the valid name of the species. This would be most unfortunate both because the name *moschatus* has never been used as a valid specific name since 1822, and because the name *reinwardtii* has been universally used as the valid name of the species to which they both apply since 1822 (see e.g. DUMÉRIL & BIBRON, 1841 : 532 ; FITZINGER, 1843 : 31 ; GÜNTHER, 1859 : 82 ; BOULENGER, 1882 : 88 ; VAN KAMPEN, 1923 : 264 ; SMITH, 1927 : 213 ; AHL, 1931 : 170 ; WOLF, 1936 : 211 ; BOURRET, 1942 : 446 ; BRONGERSMA, 1942 : 342 ; LIU & HU, 1961 : 255 ; INGER, 1966 : 294 ; LIEM, 1970 : 100 ; GRANDISON, 1972 : 75 ; GORHAM, 1974 : 171 ; BERRY, 1975 : 107 ; ANONYMOUS, 1977 : 52 ; DRING, 1979 : 216 ; FROST, 1985 : 547). An action of the Commission is therefore necessary to protect the name *reinwardtii*.

(6) Accordingly, I request the International Commission on Zoological Nomenclature :

(1) to use its plenary powers to rule that the specific name *reinwardtii*, as published in the combination *Hyla reinwardtii* Schlegel, 1840(?) (: pl. 30), is to be given precedence over the specific name *moschatus*, as published in the combination *Rhacophorus moschatus* Kuhl & Van Hasselt, 1822 (: 104), by any author who considers that both specific names apply to a single biological species ;

(2) to place the specific name *reinwardtii*, as published in the combination *Hyla reinwardtii* Schlegel 1840(?) (: pl. 30), on the *Official List of Specific Names in Zoology*, with an endorsement that it is to be given precedence over the specific name *moschatus*, as published

in the combination *Rhacophorus moschatus* Kuhl & Van Hasselt, 1822 (: 104), by any author who considers that both specific names apply to a single biological species ;

(3) to place the specific name *moschatus*, as published in the combination *Rhacophorus moschatus* Kuhl & Van Hasselt, 1822 (: 104) (type-species by monotypy of *Rhacophorus* Kuhl & Van Hasselt, 1822), on the *Official List of Specific Names in Zoology*, with an endorsement that any author who considers that this name and the name *reinwardtii*, as published in the combination *Hyla reinwardtii* Schlegel, 1840(?) (: pl. 30), apply to a single biological species, is to use the latter name for this species ;

(4) to place the generic name *Rhacophorus* Kuhl & Van Hasselt, 1822 (: 104), type-species, by monotypy, *Rhacophorus moschatus* Kuhl & Van Hasselt, 1822, on the *Official List of Generic Names in Zoology*.

RÉSUMÉ

Ainsi que nous l'avons démontré ailleurs en détail (DUBOIS, 1982), le nom valide, selon le *Code*, de l'espèce d'Anoures actuellement connue sous le nom de *Rhacophorus reinwardtii* [Schlegel, 1840(?)] est en fait *Rhacophorus moschatus* Kuhl & Van Hasselt, 1822. En conséquence, il est demandé à la Commission Internationale de Nomenclature Zoologique de faire usage de ses pleins pouvoirs pour protéger le nom *reinwardtii*, très connu et d'emploi universel.

LITERATURE CITED

ANONYMOUS, 1977. – [*Systematic keys to the Amphibians of China*]. (In Chinese). Beijing, Kexue Chupanche : [i-iv] + i-v + 1-93, pl. I-XVII.

AHL, E., 1931. – Anura III. Polypedatidae. *Das Tierreich*, **55** : i-xvi + 1-477.

BERRY, P.Y., 1975. – *The Amphibian fauna of peninsular Malaysia*. Kuala Lumpur, Tropical Press : i-x + 1-130.

BOETTGER, O., 1893. – Neue Reptilien und Batrachier aus West Java. *Zool. Anz.*, **16** : 334-340.

BOULENGER, G.A., 1882. – *Catalogue of the Batrachia Salientia s Ecaudata in the collection of the British Museum*. London, Taylor & Francis : i-xvi + 1-503, pl. I-XXX.

BOURRET, R., 1942. – *Les Batraciens de l'Indochine*. Hanoï, Institut océanographique de l'Indochine : i-x + 1-547, 4 pl.

BRONGERSMA, L.D., 1942. – On two *Rhacophorus* species mentioned by Kuhl & Van Hasselt. *Arch. néerl. Zool.*, **6** : 341-346.

DRING, J.C.M., 1979. – Amphibians and Reptiles from northern Trengganu, Malaysia, with descriptions of two new geckos : *Cnemaspis* and *Cyrtodactylus*. *Bull. Brit. Mus. nat. Hist. (Zool.)*, **34** : 181-241.

DUBOIS, A., 1981. - Liste des genres et sous-genres nominaux de Ranoidea (Amphibiens Anoures) du monde, avec identification de leurs espèces-types : conséquences nomenclaturales. *Monit. zool. ital.*, (n.s.), **15**, suppl. : 225-284.

----- 1982. – Le statut nomenclatural des noms génériques d'Amphibiens créés par Kuhl & Van Hasselt (1822) : *Megophrys*, *Occidozyga* et *Rhacophorus* *Bull Mus. natn. Hist. nat.*, (4), **4** (A) : 261-280.

DUMÉRIL, A.-M.-C. & BIBRON, G., 1841. – *Erpétologie générale ou histoire naturelle complète des Reptiles*. Tome 8. Paris, Roret : i-vii + 1-792.

FITZINGER, L., 1843. – *Systema Reptilium*. Fasc. 1. *Amblyglossae*. Vindobonae, Braumuller & Seidel : 1-106 + i-ix.

FROST, D.R. (ed.), 1985. – *Amphibian species of the world*. Lawrence, Allen Press & Assoc. Syst. Coll. : [i-xv] + i-v + 1-732.

GORHAM, S.W., 1974. – *Checklist of world Amphibians up to January 1, 1970*. Saint-John, the New Brunswick Museum : 1-173.

GRANDISON, A.G.C., 1972. – Reptiles and Amphibians of Gunong Benom with a description of a new species of *Macrocalamus*. *Bull. Brit. Mus. nat. Hist. (Zool.)*, **23** : 43-101.

GÜNTHER, A., 1859. – *Catalogue of the Batrachia Salientia in the collection of the British Museum*. London, Taylor & Francis, 1858 (1859) : i-xvi + 1-160, pl. I-XII.

INGER, R.F., 1966. – The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana : Zool.*, **52** : 1-402.

KUHL, H. & VAN HASSELT, J.C., 1822. – Uittreksel uit brieven van de Heeren Kuhl en Van Hasselt, aan de Heeren C.J. Temminck, Th. Van Swinderen en W. De Haan. *Algemeene Konst- en Letter-Bode*, **7** : 99-104.

LIEM, S.S., 1970. – The morphology, systematics, and evolution of the Old World treefrogs (Rhacophoridae and Hyperoliidae). *Fieldiana : Zool.*, **57** : i-vii + 1-145.

LIU, C.-C. & HU, S.-C., 1961. – [*The tailless Amphibians of China*.] (In Chinese). Shanghai : i-xvi + 1-364, pl. I-VI + I-XXVIII.

NIEDEN, F., 1923. – Amphibia. Anura I. Subordo Aglossa und Phaneroglossa, sectio 1 Arcifera. *Das Tierreich*, **46** : i-xxxii + 1-584.

SCHLEGEL, H., 1827. – Erpetologische Nachrichten. *Isis von Oken*, **20** : 281-294.

----- 1840(?). – *Abbildungen neuer oder unvollständig bekannter Amphibien*. Düsseldorf, Arnz & Comp. Atlas : pl. 21-30.

----- 1844. – Ibid. Text : 105-141 + i-xiv.

SMITH, M.A., 1927. – Contributions to the herpetology of the Indo-Australian region. *Proc zool. Soc. Lond.*, **1927** : 199-225, pl. I-II.

STEJNEGER, L., 1907. – Herpetology of Japan and adjacent territory. *Bull. U. S. nat. Mus.*, **58** : i-xx + 1-577, pl. I-XXXV.

----- 1925. - Chinese Amphibians and Reptiles in the United States National Museum. *Proc. U. S. nat. Mus.*, **66** (25) : 1-115.

VAN KAMPEN, P.N., 1923. – *The Amphibia of the Indo-Australian archipelago*. Leiden, Brill : i-xii + 1-304.

WOLF, S., 1936. – Revision der Untergattung *Rhacophorus* (ausschliesslich der Madagaskar-Formen). *Bull. Raffles Mus* , **12** : 137-217.

Alytes, 1988, 7 (3): 105-112.

A multivariate analysis of habitat determinants for *Triturus vulgaris* and *Triturus carnifex* in north western Italy

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The distributions of *Triturus vulgaris* and *Triturus carnifex* were studied at 80 ponds in north western Italy, in relation to a number of specific habitat features.

To establish what ecological characters can discriminate between used and unused breeding sites, several environmental factors were measured at each of these ponds and analyzed by multivariate methods. Discriminant variables for both species are : open water surface, percent vegetation around the pond, terrestrial habitat occurring near the pond, age of the pond and human interference. For *T. carnifex* both pond depth and surface also emerged as discriminant factors.

Differences between breeding site characteristics for the two species can be summarized as follows : *T. carnifex* prefers larger and deeper ponds.

T. carnifex is present with *T. vulgaris* only in deep ponds, larger and with more open water surface.

INTRODUCTION

With respect to habitat preferences, *Triturus vulgaris* and *Triturus carnifex* are among the most selective Amphibian species found in Piedmont (north western Italy) (PAVIGNANO & GIACOMA, 1986).

T. carnifex, formerly considered an Italian endemic subspecies of *T. cristatus*, actually represents a separate species, like all other "subspecies" of the crested newt (BUCCI-INNOCENTI et al., 1983).

Even though habitat features may well influence the distribution of newt species, only a few studies on the characteristics of breeding sites are available. These studies, however, did not make it possible to predict which environmental features may be responsible for the choice of breeding sites, at least in a general and comparable way (GIACOMA, 1985).

What is known, is that *Triturus vulgaris* is present in a wide range of pond habitats, while *T. cristatus* is more specialized, preferring larger and deeper ponds (HAGSTRÖM, 1979; DOLMEN, 1983a). DOLMEN (1983a) assumes that the warty newt requires the open water with a minimum of 1 m depth.

BELL (1970) and BEEBEE (1973) consider small pools to be typical smooth newt breeding sites in respect to warty.

Both smooth and warty newts tend to be associated with well-weeded sites, which give spawning places as well as food and cover from predators. However, they can also be found in ponds without vegetation (FUHN & FREYTAG, 1961 ; DOLMEN, 1983a).

T. cristatus is only occasionally found in the absence of *T. vulgaris* (BELL, 1979 ; PRESTT et al., 1974). Where they coexist in the same pond, *T. vulgaris* is nearly always more abundant than *T. cristatus* (BELL, 1979 ; GLANDT, 1978, 1982). Warty newts prefer ponds with a high proportion of open water surface (COOKE & FRAZER, 1976).

Concerning water quality, *T. cristatus* is apparently far less tolerant of acidic waters than *T. vulgaris*, and rarely breeds in more acidic than neutral conditions (CREED, 1964 ; HAGSTRÖM, 1979), even if FUHN & FREYTAG (1961), OKLAND (1979) and HAGSTRÖM (1979) found *T. cristatus* breeding in acid waters. The smooth newt can be present in metal-rich waters, particularly in those with a high calcium content. Both species, however, are common in hard waters (COOKE & FRAZER, 1976).

The two species therefore show a wide ecological amplitude with respect to water qualities and pond types.

In this study I have carried out multivariate analysis to identify which habitat features are characteristic for *T. vulgaris* and *T. carnifex* (ecological variables for *T. carnifex* have been compared with *T. cristatus* ones, because *T. carnifex* is the nearest species to *T. cristatus* as regards systematic data) and also to point out which ecological factors make it possible to differentiate used and unused breeding sites into separate groups.

I have also tried to quantify ecological variables by using statistical data that can be generalized and compared with those from different geographic areas.

Multivariate analysis has long been used for ecological studies in general (ALATALO & ALATALO, 1977 ; ORLOCI, 1966), and, i.e., for bird communities (RICE et al., 1983 ; WILLIAMS, 1978). BEEBEE (1983) used discriminant analysis to identify the most important ecological features for five amphibian species. PAVIGNANO et al. (1989) described the use of several methods of multivariate analysis applied to amphibian communities.

MATERIALS AND METHODS

During the early spring of four consecutive years (amphibian breeding seasons from 1985 through 1988), 80 ponds were sampled at three separate areas in north western Italy (Piedmont).

All sites are temporary ponds, either located in fields or in deciduous mesophilous woodlands. Most of them are artificial ponds.

Field methods employed to identify the use of ponds by amphibian species, or to measure various habitat parameters, have already been described in a previous work (PAVIGNANO & GIACOMA, 1986). Ponds were classified by the following parameters : (1) surface area, (2) depth, (3) extent of aquatic vegetation cover, (4) percent of vegetation around the pond (vegetation covering the ground around the pond), (5) age of the pond, (6) pH, (7) water hardness, (8) NO_2^-, (9) NO_3^-, (10) NH_4^+, (11) H_2S, (12) PO_4^{---} (continuous variables), (13) type of terrestrial habitat occurring near the pond (deciduous woodland, arable, meadow, scrub) and (14) level of human interference (discreet variables).

Level of human interference was estimated by observing the various kinds of human activity, and giving to each of them a score : 0 = no activity ; 1 = water used for home purposes ; 2 = water used for field irrigation ; 3 – periodic mowing of edges by farmers ; 4 = cleaning of edges and shaping of bottom ; 5 = full artificial dry-up.

Chemical water parameters were measured by (FARMATRON) volumetric kits on field ; pH was measured with a portable HANNA HI 8424 pH Meter, fitted with an automatic temperature compensator. Kits sensitivity was : water hardness 0 – 6°F, NO_3^- 0 – 10 mg/l, NO_2^- 0 – 0.05 mg/l, NH_4^+ 0 – 0.05 mg/l, H_2S 0 – 0.5 mg/l, PO_4^{---} 0 – 0.01 mg/l.

Discriminant analysis is a multivariate technique capable of classifying and predicting : it allows to distinguish between the groups so that future subjects may be correctly grouped. Discriminant analysis, together with multivariate variance analysis and cluster analysis, is therefore a method based on the differences among groups of objects. Only discriminant analysis, however, gives either the classification or the predictivity of the classification itself.

Discriminant analysis was carried out using SYSTAT Package.

RESULTS

In the studied area, *T. vulgaris* inhabits 56 ponds (70 % of the total) ; in 35 of these (44 % of the total), *T. carnifex* was also found. The latter species, therefore, was never encountered alone.

Used and unused breeding sites for each of the two species were studied by discriminant analysis (fig. 1 ; Tables I and II).

Figure 1 demonstrates how the discriminant function separates habitats according to the presence or the absence of newt populations.

Group centroids are the average discriminant scores for each group. Transformation of WILKS' lambdas into χ^2 values (Table I) shows that all the discriminant functions obtained are statistically highly significant.

In Table II it is shown by the criterion of classification accuracy, that success ranged from 94 % of sites being correctly allocated in the case of *T. vulgaris*, to 92 % for *T. carnifex*. Three ponds apparently suitable for *T. vulgaris*, and three for *T. carnifex* were inhabited by no newt. Five ponds apparently suitable for both species were inhabited only by *T. vulgaris*. This may depend in the first case on the occurrence of geographical barriers (i.e. a large street, a hill). In the second case, the absence in two sites of *T. carnifex* may be explained by the relatively small pond area being at least 1 meter deep. 5 % of unsuitable ponds were inhabited by *T. vulgaris*, 8 % by *T. carnifex*, 14 % by both species.

Significant variables for both species are : open water surface, percentage of vegetation around the pond, age of the pond, terrestrial habitat occurring near the pond, and level of human interference. For *Triturus carnifex* only, depth and surface of the pond also proved significant.

Water chemical characteristics proved to be non-significant (values of these variables do not significantly differ among the various ponds) (Table III).

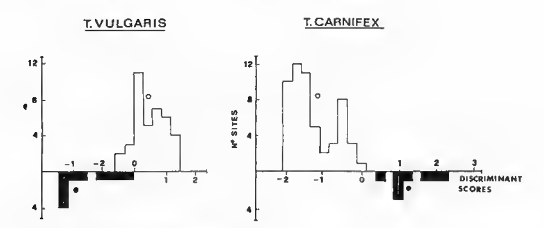


Fig. 1. – Discriminant grouping patterns.

Sites are grouped at interval widths of .2 units.

Sites without species are grouped above the discriminant score line and those with the species are below.

○ and ● represent group centroids.

In order to discriminate between ponds used by *T. vulgaris* only, or by *T. vulgaris* and *T. carnifex* together, another discriminant analysis was carried out only on used ponds (fig. 2, Tables I and II).

In this case the difference between groups also proved highly significant.

The most important variables are : surface area, depth and open water surface. *T carnifex* is present with *T. vulgaris* only in deeper and larger ponds, having less aquatic vegetation.

The distribution of both species in relation to the habitat characteristics of breeding sites is shown in Table IV.

T. carnifex was found in 35 out of 50 large sites (area of 100-1000 m^2 and > 1000 m^2), in 35 out of 55 deep ponds (depth of 50-100 cm and > 100 cm) and in 20 out of 28 sites with little aquatic vegetation (< 20 %).

Table I. – Significance of discriminant analysis.

Species	Canonical correlation	λ Wilks	χ^2	Significance
T. vulgaris	0.652	0.574	30 506	0.000
T. carnifex	0.639	0.592	28.835	0.000
T. vulgaris and *T. carnifex*	0.825	0.319	30.847	0.000

Table II. – Success rates of discriminant classification.

Site numbers observed refer to those known to be used (+) or unused (−) by the two species. Predicted numbers are shown as those expected to be used or unused on the basis of discriminant function.

% correct refers to site numbers observed/site numbers predicted.

Species	Site numbers observed		Site numbers predicted		% correct
	+	−	+		
T. vulgaris	56	24	59	21	94
T. carnifex	35	45	38	42	92
T. vulgaris and *T. carnifex*	35	45	40	40	87

Table III. – Chemical water factors.

Variables (n sites = 80)	M	Min	Max	SD
pH	7.1	6.5	7 5	0.30
Water hardness (°F)	12.5	12.0	14.0	0.01
NO_2 (mg/l)	0.05	0.00	0 06	0.14
NO_3^- (mg/l)	0.02	0.00	0.01	0.01
NH_4^+ (mg/l)	0.02	0.00	0.02	0.01
H_2S (mg/l)	0.05	0.01	0 13	0.02
PO_4^{--} (mg/l)	0.01	0.00	0.02	0.01

Table IV. – Characteristics of breeding sites and presence of newts.

Variables	All sites	Sites with only *T. vulgaris*	Sites with *T. vulgaris* and *T. carnifex*
Surface (m^2)			
< 50	17	11	–
50-100	13	10	–
100-1000	25	17	17
> 1000	25	18	18
Depth (cm)			
< 50	25	21	–
50-100	29	20	20
> 100	26	15	15
% extent of aquatic vegetation cover			
< 20	28	21	20
20-50	20	13	13
> 50	32	22	2
Total numbers of sites	80	56	35

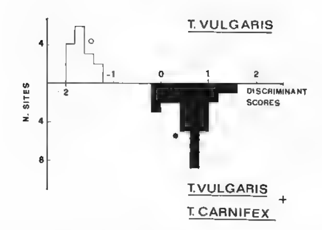


Fig. 2. – Discriminant grouping patterns. Sites with *T. vulgaris* and sites with both *T. vulgaris* and *T. carnifex*.

T. vulgaris seems to be indifferent either to the extent or the depth of the ponds, requiring in any case a great quantity of aquatic vegetation. Deciduous woodlands and scrubby terrestrial habitat structure are optimal for both species.

The breeding sites preferred by the two species are ponds with heterogeneous vegetation and with low level of human interference.

Discussion

The use of discriminant analysis made it possible to distinguish between habitats used and not used by the two species of *Triturus* as breeding sites. The most important habitat characters for both species are : extent of aquatic vegetation cover, vegetation around the pond, terrestrial habitat, human interference and age of pond.

For *T. carnifex* only, pond depth and surface are also discriminant.

The chemical parameters of studied ponds, in opposition to northern Europe (Cooke & Frazer, 1976), do not vary so much to influence the distribution of newts.

In northern Europe *T. cristatus* seems to prefer bog localities or farming/clay areas and to be nearly absent from lakelets, forest ponds, rock-pools and reed-bed tarns while *T. vulgaris* occupies a wide range of locality types (Dolmen, 1980). In northern Italy both species avoid the ponds in fields, because of the strong human interference.

According to Cooke & Frazer (1976) and Dolmen (1983a) differences between breeding sites of the two species would be the following: both species tend to colonize the well-weeded sites, which give spawning places, food and cover from predators ; but *T. cristatus* prefers large, deep ponds, with more open water surface.

T. vulgaris breeds in a wider range of habitats ; for this reason it may be considered a "more eurycious" (that is, it shows a wider ecological amplitude as regards pond types) species than *T. carnifex*.

Many ponds are apparently suitable for both species and coexistence is frequently observed, but only in deeper and larger ponds.

DOLMEN (1980, 1983b), GRIFFITHS (1987), GRIFFITHS & MYLOTTE (1987), HAGSTRÖM (1979) and STRIJBOSCH (1979, 1980) observed in syntopic populations a microhabitat partitioning : *T. cristatus* occupies the centre of the pond, where it is deeper and there is more open water surface.

Various studies have shown habitat features for these two species, but the results are often difficult to compare because of considerable differences in the methodological approach. These results are often very complex and different ; the use of statistical analysis could give values in a general and comparable way.

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LITERATURE CITED

ALATALO, R.V. & ALATALO, R.H., 1977. – Components of diversity multivariate analysis with interaction. *Ecology*, **58** : 900-906.

BEEBEE, T.J.C., 1973. – Observations concerning the decline of British Amphibians. *Biological conservation*, **5** : 20-24.

----- 1985. – Discriminant analysis of amphibian habitat determinants in south-east England. *Amphibia-Reptilia*, **6** : 35-43.

BELL, G., 1970. – The distribution of amphibians in Leicestershire, with notes on their ecology and behaviour. *Trans. Leicester Lit. Soc.*, **54** ; 122-143.

----- 1979. – Populations of crested newts, *Triturus cristatus*, in Oxfordshire, England. *Copeia*, **1979** : 350-353.

BUCCI-INNOCENTI, S., RAGGHIANTI, M. & MANCINO, G., 1983. – Investigation of karyology and hybrids in *T. boscai* and *T. vittatus* with a reinterpretation of the species groups within *Triturus* (Caudata : Salamandridae). *Copeia*, **1983** : 662-672.

CREED, K., 1964. – A study of newts in the New Forest. *British J. Herp.*, **3** : 170-181.

COOKE, A.S. & FRAZER, J.F.D., 1976. – Characteristics of newt breeding sites. *J. Zool. Lond.*, **178** . 223-236.

DOLMEN, D., 1980. – Distribution and habitat of the smooth newt *Triturus vulgaris* and the warty newt *Triturus cristatus* in Norway. *Proceedings of European Herpetological Symposium* · 127-139.

----- 1983a. – A survey of the Norwegian newts (*Triturus*, Amphibia), their distribution and habitat. *Meddelelser fra Norsk Viltforskning*, **3** (12) : 1-71.

----- 1983b. – The rhythms and microhabitat preference of the newts *Triturus vulgaris* and *Triturus cristatus* at the northern border of their distribution area. *J. Herp.*, **17** : 23-31.

FUHN, I.E. & FREYTAG, G.E., 1961. – Taxonomische und okologische studien über *Triturus cristatus* in Rumänien. *Zoologischer Anzeiger*, **5-6** : 159-173.

GIACOMA, C., 1985. – The ecology and distribution of newts in Italy. *Ann. Ist. Mus. Zool. Univ. Napoli*, **26** : in press.

GLANDT, D., 1978. – Notizen zur Populationsökologie einheimischer Molche (Gattung *Triturus*). *Salamandra*, **14** : 9-28.

----- 1982. – Abundanzmessungen an mitteleuropäischen *Triturus*-Populationen (Amphibia, Salamandridae). *Amphibia-Reptilia*, **4** : 317-326.

GRIFFITHS, R.A., 1987. – Microhabitat and seasonal niche dynamics of smooth and palmate newts, *Triturus vulgaris* and *T. helveticus*, at a pond in mid-Wales. *J. anim. Ecol.*, **56** : 441-451.

GRIFFITHS, R.A. & MYLOTTE, V.J., 1987. – Microhabitat selection and feeding relations of smooth and warty newts, *Triturus vulgaris* and *T. cristatus*, at an upland pond in mid-Wales. *Holarctic Ecology*, **10** : 1-7.

HAGSTRÖM, T., 1979. – Population ecology of *Triturus cristatus* and *Triturus vulgaris* (Urodela) in SW Sweden. *Holarctic Ecology*, **2** : 108-114.

OKLAND, J., 1969. – Om forsuring av vassdrag og betydming av surhetsgraden (Ph) for fiskens noeringsdry i ferskvam. *Holarctic Ecology*, **22** : 140-147.

ORLOCI, L., 1966. – Geometric models in ecology I. The theory and application of some ordination methods. *J. Ecol.*, **54** : 193-215.

PAVIGNANO, I. & GIACOMA, C., 1986. – Osservazioni sulla distribuzione e sul comportamento riproduttivo degli anfibi presenti in un'area della pianura piemontese. *Riv. piem. St. nat.*, **7** : 153-171.

PAVIGNANO, I., GIACOMA, C. & CASTELLANO, S., 1989. – A multivariate analysis of amphibian habitat determinants in north western Italy. *Amphibia-Reptilia*, submitted.

PRESTT, I., COOKE, A.S. & CORBETT, K.F., 1974. – British amphibians and reptiles. *In* : D.L. HAWKSWORT (ed.), *The changing flora and fauna of Britain*, London, Academic Press : 1-461.

RICE, T.C., OHMART, R.D. & ANDERSON, B.S., 1983. – Habitat selection attributes of an avian community : a discriminant analysis investigation. *Ecol. Mong.*, **53** : 263-290.

STRIJBOSCH, H., 1979. – Habitat selection of amphibians during their aquatic phase. *Oikos*, **33** : 363-372.

----- 1980. – Habitat selection by amphibians during their terrestrial phase. *Brit. J. Herp..*, **6** : 93-98.

WILLIAMS, J.D., 1978. – Multivariate analysis of avian vocalization. *J. theor. Biol.*, **74** : 83-107.

Un cas d'accouplement dorsal inverse chez *Rana perezi*

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We found a couple of *Rana perezi* in inverse dorsal amplexus among a dense and vocally active population during the spawning period, in the region of Tourém (north of Portugal).

We make comments about the possible ethological and evolutionary meaning of this behaviour.

La récente description d'un cas d'accouplement ventral chez *Rana* kl. *esculenta* (Polls Pelaz, 1987) nous a amenés à faire connaître un autre cas d'accouplement anormal que nous avons observé chez *Rana perezi*.

Cette observation a été faite pendant le jour (17h, 20 mai 1988, temp. de l'air : 24° C), au sein d'une population abondante et dense de *Rana perezi* à Tourém (nord du Portugal).

Le couple en question se trouvait en accouplement dorsal inverse. Le mâle sur le dos de la femelle, mais sa tête tournée vers la partie postérieure de sa partenaire, la maintenait fortement embrassée dans la région inguinale.

Le couple a été repéré dans l'eau en compagnie de nombreux autres mâles qui coassaient et de quelques autres couples en amplexus dorso-axillaires normaux. Nous l'avons placé sur le sol, pour la photo. Il y est resté de lui-même pendant environ une demi-heure avant de retourner dans l'eau, toujours dans ce même amplexus.

Il nous semble évident que cet amplexus inversé est le résultat d'une "erreur" justifiée probablement par la grande densité de la population sexuellement active.

Dans ces conditions, comme cela a déjà été observé auparavant (Angel, 1947 ; Noble, 1954 ; etc.), les mâles sont souvent saisis d'une "fureur génésique" qui leur fait saisir, pour s'accoupler, un objet quelconque ou une espèce animale parfois fort différente de la leur.

Cette circonstance peut conduire à la formation de couples aberrants et ceux-ci peuvent même dans certains cas être stables (Delsol, 1986).

On peut admettre que dans un premier essai le mâle ait essayé l'amplexus axillaire normal, mais qu'en face d'une réaction de rejet de la femelle, ou parce qu'il y avait déjà un autre mâle en amplexus, il ait pris, après l'abandon du rival, la position décrite ici.

Il se peut que l'ambiance dense et vocalement active où le couple se trouvait, et peut-être une probable fatigue de la femelle due à des amplexus ou des pontes préalables, aient fonctionnés comme facteurs inhibiteurs de la réaction naturelle de rejet par la femelle.

On ne doit pas exclure non plus la possibilité que l'amplexus, bien qu'inguinal et inversé, ait contribué lui-même à réduire la réaction de rejet. Il est probable que, même dans ces conditions, les interactions qui jouent dans la reconnaissance des partenaires sexuels – les mouvements respiratoires, les vibrations thoraciques, la rythmicité de l'amplexus (Rabb, 1973 ; Duellman & Trueb, 1986) – aient été effectives, bien que d'une façon plus atténuée.

Les manifestations épisodiques d'amplexus aberrants peuvent être plus ou moins fréquentes dans les cas de mâles jeunes, dont les dimensions sont très différentes de celles des femelles avec lesquelles ils veulent s'accoupler.

Dans ces accouplements aberrants, plus que le comportement des mâles, ce qui est biologiquement intéressant est l'apparente réduction de la réaction de rejet de la femelle, dont il serait intéressant de mieux préciser à l'avenir les raisons globales.

En raison de la haute spécificité des interactions de reconnaissance des partenaires sexuels au moment de l'amplexus (Rabb, 1973), celles-ci constituent un mécanisme important d'isolement pré-reproducteur (Wells, 1977).

Quelque rupture transitoire de l'efficacité de ce mécanisme peut, à l'occasion, prendre une signification genétique-évolutive, car, en certaines circonstances (notamment de sympatrie et de synchronisation des cycles reproducteurs des espèces en présence), elle peut aboutir à des phénomènes d'hybridation.

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Références bibliographiques

Angel, F., 1947. – *Vie et mœurs des Amphibiens*. Paris, Payot : 1-317.
Delsol, M., 1986. – Les types fondamentaux de la reproduction. *In* : P.-P Grassé (dir.), *Traité de Zoologie*, T. XIV (1B), *Batraciens*, Paris, Masson : 321-388.
Duellman, W.E. & Trueb., L., 1986. – *Biology of Amphibians*. New York, McGraw – Hill : i-xix + 1-670.
Noble, G.K., 1954. – *The biology of the Amphibia*. New York, Dover : 1-577.
Polls Pelaz, M., 1987. – Un accouplement ventral chez *Rana* kl. *esculenta*. *Alytes*, **6** : 85-87.
Rabb, G.B., 1973. – Evolutionary aspects of the reproductive behavior of frogs. *In* : J.L. Vial (ed.), *Evolutionary biology of Anurans*, Columbia (U.S.A.), Univ. Missouri Press . 213-227.
Wells, K.D , 1977. – The courtship of frogs *In*: D.H. Taylor & S.I. Guttman (eds.), *The reproductive biology of Amphibians*, New York, Plenum Press : 233-262.

Developmental rate of *Rana* synkl. *esculenta* (Ranidae, Anura) embryos from different crosses: consequences on the evolution of the populations

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Crosses between different members of the *Rana* synkl. *esculenta* show a great variability concerning ontogenetic parameters. For this study developmental rate until stage 25 (Gosner, 1960), v(25), and time interval to pass through this stage, dt(25), are used to measure differences between progeny of naturally observed combinations. For *esculenta* × *esculenta* progeny, mortality at this stage is very high; often all larvae of a cross die. Retardation of gene expression and nucleocytoplasmic incompatibility in early development could be the explanation of the differences in developmental rate. Mortality of *esculenta* homotypic crosses could be related to clone selection and not to accumulation of lethal genes : evolution by increasing variation and selection is not inhibited by reproduction without recombination. Clonally inherited genomes of *esculenta* that show high vitality in combination with *lessonae* genomes, give inviable progeny in homotypic crosses.

Introduction

European green frogs (*Rana* synkl. *esculenta* Linné, 1758) (Dubois & Günther, 1982) are a very particular group of vertebrates. This group inludes two "good" species (*Rana ridibunda* Pallas, 1771 ; *Rana lessonae* Camerano, 1882) and their hybrid (*Rana* kl. *esculenta* Linné, 1758) (Berger, 1967 ; Tunner, 1973). *Rana* kl. *esculenta* remains in the hybrid state by a particular type of gametogenesis called hybridogenesis (Tunner, 1974).

Consequently a frog with hybrid somatic cells produces gametes which are in their nucleotic and also in major part of their cytoplasmic component of parental type (generally *ridibunda*) (Vogel & Chen, 1976 ; Graf, Karch & Moreillon, 1977) Nevertheless substances produced by somatic cells and transferred into the oocytes, like yolk, might have a hybrid nature and cause the differences observed between these eggs and eggs of the corresponding parental species concerning development and survival of progeny.

Green frogs populations not only contain individuals of different species, but also individuals of different ploidy levels. They can produce a great genetic variety in gametes and still a greater genetic variety in zygotes should be observed. But investigations on genotypes

of frogs found in natural populations show only certain genotypes, the others having been eliminated before or shortly after metamorphosis (GÜNTHER, 1983).

Crossing experiments among green frogs have shown an important mortality and a high number of anomalous larvae in certain combinations (BERGER, 1967 ; OGIELSKA-NOWAK, 1985). Developmental anomalies can be of two kinds : disturbances can be of short term for the population, like morphological anomalies of embryos and larvae and mortality at different developmental stages ; or they can be long term defaults modifying survival and fertility of adults.

Evolutionary success of asexual, clonal and hemiclonal species is doubtful (MULLER, 1932 ; MAYNARD SMITH, 1974). Asexual and clonal reproduction permits a quicker diffusion of an established genotype, but lowers variation and elimination of deleterious mutant alleles by default of recombination.

For this work I have chosen stage 25 (GOSNER, 1960), since larvae of this developmental stage are particularly affected in green frogs (BERGER, 1967 ; BLANKENHORN, HEUSSER & VOGEL, 1971 ; BINKERT, 1981). Ontogenetic events occurring in this stage seem to play an important part in the success of the different crossings. Similar developmental disturbances have been observed in green frog larvae from different populations all over Europe. Indications from these developmental patterns for evolution of hemiclonally reproducing *esculenta* will be discussed.

MATERIAL AND METHODS

The green frogs of this study came from eastern Austria (Seewinkel, Burgenland ; Lobau and Donauinsel, Vienna) and from central France (Brenne, Indre) (Table I). Parents of the crosses and tadpoles are kept in the collection of the Paris Muséum national d'Histoire naturelle (MNHN 1986.1763-1790) or in the author's collection.

Eggs were obtained from frogs without hormone injection so as to avoid damaging the eggs. Generally couples were taken in the natural environment (crosses number 1 – 10, 12 – 14 and 17 – 19) or reproductively active frogs were put together in the laboratory where they spontaneously amplected (crosses number 11, 15, 16 and 20). The whole clutches (900 to 3000 eggs) were transferred to indoor plastic containers (40 × 60 × 20 cm) and divided into portions of 20 to 30 eggs to assure oxygen supply. The embryos and larvae were reared at indoor temperature (water temperature : 18-22°C). About 300 small embryos were kept in a container. Development was controlled with a dissecting microscope and determined following the staging table of GOSNER (1960). When the larvae reached stage 25, the number of surviving larvae was limited to 50 by container (2 larvae / liter of water). They were fed a mixture of dried *Urtica dioica* and Tetra Min fish food. Dead and anomalous larvae were fixed in 4 % formalin.

Rate of development, v(25), is expressed as 100 divided by time in days to stage 25 (1 / T × 100) for the first embryo which reached this stage. This measurement gives the *optimal* development rate observed for a specific cross. The period during which stage 25 larvae could be observed, dt(25), is given in days. For every kind of crosses, the mean (m), the standard deviation (s) and the coefficient of variation following HALDANE (1955), V_H (DE-

LAUGERRE & DUBOIS, 1985), were calculated. The different crosses were compared by the non-parametric Mann-Whitney U-test (ELLIOTT, 1971). The correlation coefficient r was calculated with the statistical program package SPSSx (SCHUBÖ & UEHLINGER, 1986).

RESULTS

The two parental species differ in their developmental rates (Table I) (U-test : $U=0$; $n_1=4$; $n_2=4$; $p<0.05$). *Rana ridibunda* progeny takes a longer time to reach stage 25, but usually larvae get through this stage quickly. *Rana lessonae* embryos develop more quickly until stage 25, but a greater variation concerning the time requested to pass through this stage is observed.

Progeny of *esculenta* female × *esculenta* male shows a high variation in developmental rate ($m=8.30$; $s=1.78$; $n=6$; $V_H=21.45$) ; the extremes cover the developmental rates of progeny of *Rana ridibunda* (U-test : $U=9$; $n_1=4$; $n_2=6$; $p>0.05$) and *Rana lessonae* (U-test : $U=4$; $n_1=6$; $n_2=4$; $p>0.05$). The interval during which stage 25 larvae can be observed is very large.

Developmental rate of *lessonae* female by *esculenta* male embryos ($m=7.42$; $s=0.39$; $n=2$) resembles that of *Rana ridibunda* progeny ($m=7.16$; $s=0.42$; $n=4$), but stage 25 larvae are present during a much longer period. The progeny of the reciprocal cross (*esculenta* female × *lessonae* male) has a very high developmental rate ($m=10.07$; $s=1.01$; $n=3$) which is similar to that of *Rana lessonae* embryos ($m=10.33$; $s=0.98$; $n=4$). Here too the time interval during which stage 25 larvae are observed is very large.

At stage 25, especially in homotypic crosses of *esculenta* female × *esculenta* male, a high mortality of tadpoles was observed. All larvae of crosses (8) and (11) died ; only a few developed small buds of the hindlimbs. The larvae showed no particular anomalous features, but they were transparent and smaller than viable tadpoles of the same age. High lethality was observed only in *esculenta* homotypic crosses.

For green frogs from Austria, developmental rate is highly correlated with the date of reproduction ($r=0.61$; $f=14$; $p<0.01$). *Rana ridibunda*, which generally reproduces earlier in the year, has a lower developmental rate than *Rana lessonae* which is the latest of the green frogs to reproduce. In France, breeding of green frogs is earlier in the year than in Austria, but developmental rates of the crossings correspond to what was observed in Austrian larvae.

DISCUSSION

Stage 25 in anuran development is the product of embryogenesis and the starting point for larval development which gives the basis of parameters at metamorphosis (age, size) (WILBUR & COLLINS, 1973 ; TRAVIS, 1981). In the beginning stages, development depends on maternal factors stocked in the oocyte. Only in late blastula stages are paternal genes expressed (WRIGHT & MOYER, 1968). This is often a critical point in hybrid ontogeny and various disturbances can be observed : development stops in these stages or expression of pa-

Table I. – Developmental rate of different crosses within *Rana* synkl. *esculenta*. (L, localities : V, Vienna ; B, Burgenland ; I, Indre ; date, date when eggs were laid ; M, male ; F, female ; v(25), rate of development ; I(25), age interval in days of stage 25 larvae ; dt(25), time interval during which stage 25 (GOSNER, 1960) tadpoles were observed ; R, *Rana ridibunda* ; E, *Rana* kl. *esculenta* ; L, *Rana lessonae* ; m, mean ; s, standard deviation ; V_H, HALDANE coefficient of variation).

Cross	L	Date	M	F	v(25)	I(25)	dt(25)
(1)	V	11.5.1983	R	R	7.69	13 - 15	2
(2)	V	11.5.1983	R	R	6.67	15 - 17	2
(3)	V	11.5.1983	R	R	7.14	14 - 26	12
(4)	V	6.5.1984	R	R	7.14	14 - 16	2
					m=7.16		m=4.50
					s 0.42		s=5.00
					V_H=5.87		V_H=111.11
(5)	V	28.4.1983	R	E	5.26	19 - 81	62
(6)	B	28.5.1983	E	E	6.67	15 - 49	34
(7)	B	28.5.1983	E	E	9.09	11 - 59	48
(8)	B	28.5.1983	E	E	11.11	9 - 18	9
(9)	B	6.6.1984	E	E	7.14	14 - 27	13
(10)	B	17 6.1984	E	E	9 09	11 - 16	5
(11)	I	4.5.1986	E	E	6.67	15 - 50	35
					m=8 30		m–24.00
					s=1.78		s=17.33
					V_H=21.45		V_H 72.26
(12)	B	28.5.1983	L	E	10.00	10 - 35	25
(13)	B	28.5 1983	L	E	9 09	11 - 56	45
(14)	B	28 5.1983	L	E	11.11	9 - 23	14
					m=10.07		m=28.00
					s=1 01		s=15.72
					V_H=10.05		V_H=56.13
(15)	I	5.5.1986	E	L	7.69	13 - 50	37
(16)	I	7.5.1986	E	L	7.14	14 - 49	35
					m 7 42		m 36.00
					s=0.39		s=1.41
					V_H 5 24		V_H 3.93
(17)	B	31.5.1983	L	L	11.11	9 - 23	14
(18)	B	31.5.1983	L	L	9.09	11 - 47	36
(19)	B	31.5.1983	L	L	11.11	9 - 17	8
(20)	I	8.5.1986	L	L	10.00	10 - 34	24
					m=10.33		m=20.50
					s=0.98		s=12.26
					V_H 9.46		V_H=59.80

ternal genes is delayed or inhibited (WHITT, CHO & CHILDERS, 1972) ; morphological anomalies (e.g. exogastrulae : DELARUE et al., 1985 ; ELINSON, 1981 ; HENNEN, 1963 ; HERTWIG, RUHLAND & WEISS, 1958) can be the epigenetic reflection of these disturbances. Usually the embryonal phase ends without new disturbances, but anomalous embryos can be observed in tailbud stage or later ; these morphological disturbances should be regarded as a consequence of difficulties in the gastrula phase. In stage 25 transition to active larval life takes place, which includes physiological modifications (nutrition).

Different time intervals required to reach stage 25 (Table I) reflect events in embryonic development (retardations, etc.). Variation in the time necessary to pass through stage 25 (Table I) can be related to hybrid genome constitution of *esculenta* progeny and might therefore reflect developmental difficulties in the transition from embryonic to larval life. In *lessonae* larvae it might rather be a consequence of genetic variation, perhaps due to lack of competition with *esculenta* larvae in mixed populations.

In the hybridogenetic taxon *esculenta*, gametogenesis results in oocytes with a non-recombined genome which consists entirely of chromosomes of one parental type (*ridibunda* : VOGEL & CHEN, 1976 ; GRAF, KARCH & MOREILLON, 1977 ; or *lessonae* : GÜNTHER 1983 ; BERGER & GÜNTHER, 1988). To a large extent, their cytoplasm resembles that of the oocytes of this parental species.

Zygotes produced by homotypic *esculenta* crosses have been shown to contain two sets of the same parental genome and a corresponding cytoplasm, like in homotypic crosses of the parental species. But the genomes did not pass through recombination. On the other hand, when *esculenta* eggs are fertilized by *lessonae* sperm, the resulting zygotes have a hybrid genome and a cytoplasm of *ridibunda* type. This could appear to be a rather unbalanced situation, but in fact this combination is very successful.

The observations on different crosses of green frogs can be studied in the light of their cytogenetic constitution. The rather homogeneous developmental rate of the crosses where parental species are involved (Table I) is interpreted as a consequence of recombination and gene flow in these populations. Only *ridibunda* tadpoles get through stage 25 very quickly (Table I). In *lessonae* crosses, tadpoles usually have delayed development at these stages. On the other hand, the variation in developmental rate in *esculenta* homotypic crosses has been interpreted as a consequence of clonal inheritance of the genomes in the involved taxon which should lead to accumulation of deleterious genes (BERGER, 1976 ; GRAF & MÜLLER, 1979 ; HOTZ, 1983 ; BINKERT, BORNER & CHEN, 1982). Embryos of these crosses are also affected by various morphological anomalies ("*esculenta* developmental syndrom", OGIELSKA-NOWAK, 1985 ; OHLER, 1987).

Only in homotypic *esculenta* crosses, the developmental disturbances can be lethal for all larvae within a cross. These lethal crosses are very numerous in populations where *lessonae* and *esculenta* live in sympatry and where *esculenta* entirely depends upon *lessonae* for its reproduction, whereas they are less important in populations where *lessonae* is absent. In the latter, the genetical basis for hybrid state conservation is different, and triploid *esculenta* play an important role in producing gametes of *lessonae* type (GÜNTHER, 1983).

Very similar developmental phenomena concerning homotypic *esculenta* crosses are observed in geographically distant populations (BERGER, 1967 ; BLANKENHORN, HEUSSER & VOGEL, 1971 ; GÜNTHER, 1973 ; OHLER, 1987 ; TUNNER, 1979, 1980 ; WIJNANDS, 1979). If

they are related to genetic load of *esculenta* hemiclones, it would mean a very wide distribution of these lineages. Also, genetic load does not seem to be superior in green frogs from clonal lineages where recent hybridization can be excluded (HOTZ, 1983). Various hypotheses about evolutionary dead-end or success of clonally (asexual) reproducing species have been or can be proposed ; particularly two of them are worthy of discussion : MULLER's ratchet mechanism and a model of evolution in asexual populations.

MULLER's ratchet mechanism (1932) explains that in asexually reproducing species the load of mutations cannot decrease below that already present in the least loaded clone, but that it can increase. In consequence, mutations, that should be mostly deleterious ones, will accumulate in clonally inherited genomes and such lineages are rather condemned to extinction over long term evolution.

This is true within a clone, but not for a clonally reproducing "species" which includes a series of different clones. There are two sources for the variation among clones : multiple origins and mutation (ANGUS & SCHULTZ, 1979). Recombination provides a much greater variation than mutation alone can do. This is the major advantage of sexual reproduction. It accelerates evolution very substantially, particularly in large populations (MAYNARD SMITH, 1974). But in sexually reproducing species a given genotype is lost for the next generation and is unlikely to reappear. Clonal inheritance of the genome prevents the loss of a certain combination of genes. This can be favorable despite the shortage of variation, for example in small colonizing populations. Asexual reproduction can assure the rapid increase of a given genotype. As shown by mathematical models, evolution is not stopped by asexual reproduction, but evolution rate may be reduced under certain conditions (MAYNARD SMITH, 1974).

Variation in *esculenta* clonal lineages comes from primary hybridization in areas where the two parental species occur in sympatry, and from mutation. There is still an other possibility for increasing variation in regions where only *lessonae* and *esculenta* occur : some of the progeny of *esculenta* homotypic crosses can survive to sexual maturity ; these individuals may have *ridibunda* genotypes and can act as founders of new hybridogenetic lineages.

The very similar developmental pattern of *esculenta* × *esculenta* germs from populations of all over Europe reflects rather a cytoplasmic inconvenience or an incompatibility of regulatory genes than an accidental accumulation of lethal genes and their subsequent dispersion in hemiclonal lineages. In regions where primary hybridization can still occur, *esculenta* × *esculenta* crosses show a high variability in developmental pattern (BERGER, 1967). On the other hand, the variability of developmental pattern is reduced where primary hybridization founded clonal lineages long time ago (HOTZ, 1983). The different *esculenta* lineages will be selected that assure a successful development in *esculenta* × *lessonae* crossings and that assure the maintenance of the hybrid.

Lethality at stage 25 in *esculenta* homotypic crosses means an important loss of gametes for the population. But as these germs die before feeding they don't compete with vital larvae of the other combinations concerning food, and also space (crowding). As their death coincidates with the starting of feeding of the vital larvae and as green frog larvae may be cannibalistic, especially on feeble tadpoles, they could be a source of food, and their unsuccessful development would allow the transmission to these larvae of a great part of the substances of the *esculenta* oocytes.

To estimate the influence of life-history parameters of a population, the combination

of a series of facts must be considered. The loss of gametes by *esculenta* homotypic crosses can be leveled out by the subsequent consumption of the larvae by the other members of the population. This supplementary food source should favour their larval development and metamorphosis.

Hybrid embryos of *esculenta* type (from *esculenta* × *lessonae* crossings) are as successful as *lessonae* larvae in developmental rate and in passing through stage 25. In E-L populations, larvae of the two types have equal ontogenetic potential. Developmental success of larvae from homotypic *esculenta* crosses is extremely reduced. Nevertheless, the *esculenta* genetic system seems very stabilized, which permits the large radiation observed in these frogs. The maintenance of *Rana* kl. *esculenta* is assured by cytoplasmic compatibility in hybrid zygotes, success of larval development and a variety of genetic mechanisms for meiosis in different population systems.

RÉSUMÉ

Les produits des croisements réalisés entre différents membres du synklepton de *Rana* kl. *esculenta* manifestent une grande variabilité en ce qui concerne leurs paramètres ontogénétiques. Pour cette étude, deux indices, le taux de développement jusqu'au stade 25 de GOSNER (1960), v(25), et la durée de l'intervalle nécessaire pour traverser ce stade, dt(25), ont été utilisés pour mesurer les différences entre les descendances obtenues à partir de diverses combinaisons parentales observées dans la nature. La mortalité au stade 25 est très élevée dans la descendance issue des croisements homotypiques *esculenta* × *esculenta* : souvent toutes les larves d'un croisement meurent. Ces différences développementales pourraient être dues à des retardations dans l'expression de certains gènes et des incompatibilités nucléocytoplasmiques au début du développement. La mortalité observée dans les croisements homotypiques *esculenta* pourrait être due à la sélection des clones et non pas à l'accumulation des gènes léthaux : l'évolution par augmentation de la variation et sélection n'est pas supprimée par la reproduction sans recombinaison. Les génomes *esculenta* transmis de manière clonale qui montrent une vitalité élevée en combinaison avec les génomes *lessonae*, donnent une descendance inviable dans les croisements homotypiques.

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LITERATURE CITED

ANGUS, R.A. & SCHULTZ, R.J., 1979. – Clonal diversity in unisexual fish populations. *Amer. Natur.*, **115** : 531-550.

BERGER, L. 1967. – Embryonal and larval development of F1 generation of green frogs different combinations. *Acta zool. Cracoviensis*, **12** : 123-162.

----- 1976. – Hybrids of B_2 generation of European water frogs (*Rana esculenta* complex). *Ann. Zool.*, Warszawa, **33** : 201-214.

BERGER, L. & GÜNTHER, R., 1988. – Genetic composition and reproduction of water frog populations (*Rana* kl. *esculenta* Synklepton) near nature reserve Serrahn, GRD. *Arch. Nat.-schutz Landsch.-forsch.*, Berlin, **28** : 265-280.

BINKERT, J A., 1981. – *Untersuchungen uber die Letalität der inter-se-Kreuzungen von* Rana esculenta. Ph D Thesis, Universität Zürich, Schweiz : i-iii + 1-194.

BINKERT, J.A., BORNER, J. & CHEN, P.S., 1982. – *Rana esculenta* complex : an experimental analysis of lethality and hybridogenesis. *Experientia*, **38** : 1283-1292.

BLANKENHORN, H J., HEUSSER, H. & VOGEL, P., 1971. – Drei Phänotypen von Grünfröschen aus dem *Rana esculenta* Komplex in der Schweiz. *Rev. suisse Zool.*, **78** : 1242-1247.

DELARUE, M., DARRIBERE, T., AIMAR, C. & BOUCAUT, J.-C , 1985. – Bufonid nucleocytoplasmic hybrids arrested at the early gastrula stage lack a fibronectin-containing fibrillar extracellular matrix. *Roux's Arch. Dev. Biol.*, **194** : 275-280.

DELAUGERRE, M. & DUBOIS, A., 1985. – La variation géographique et la variabilité intrapopulationnelle chez *Phyllodactylus europaeus* (Reptilia, Sauria, Gekkonidae). *Bull. Mus. natn. Hist. nat.*, (4), **7** (A), n° 3 : 709-736.

DUBOIS, A. & GÜNTHER, R., 1982. – Klepton and synklepton : two new evolutionary systematics categories in zoology. *Zool. Jb. Syst.*, **109** : 290-305.

ELINSON, R.P., 1981. – Genetic analysis of developmental arrest in an amphibian hybrid (*Rana catesbeiana*, *Rana clamitans*). *Dev. Biol.*, **81** : 167-176.

ELLIOTT, J.M., 1971. – Statistical analysis of samples of benthic invertebrates. *Freshwater Biol. Assoc., Sci. Pub.*, **25** : 1-148.

GOSNER, K.L., 1960. – A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, **16** : 183-190.

GRAF, J D., KARCH, F. & MOREILLON, M.C., 1977. – Biochemical variation in the *Rana esculenta* complex. A new hybrid form related to *Rana perezi* and *Rana ridibunda*. *Experientia*, **33** : 1582-1584.

GRAF, J.D. & MÜLLER, W.P., 1979. – Experimental gynogenesis provides evidence of hybridogenetic reproduction in the *Rana esculenta* complex. *Experientia*, **35** : 1574-1576.

GÜNTHER, R., 1973. – Über die verwandschaftlichen Beziehungen zwischen den europäischen Grünfröschen und den Bastardcharakter von *Rana esculenta*. *Zool. Anz.*, **190** . 250-285

----- 1983. – Zur Populationsgenetik der mitteleuropäischen Wasserfrösche des *Rana esculenta*-Synkleptons (Anura, Ranidae). *Zool. Anz.*, **211** : 43-54.

HALDANE, J.B.S., 1955. – The measurement of variation. *Evolution*, **9** : 484.

HENNEN, S., 1963. – Chromosomal and embryological analysis of nuclear changes occurring in embryos derived from transfer of nuclei between *Rana pipiens* and *Rana sylvatica*. *Dev. Biol.*, **6** : 133-183.

HERTWIG, G., RUHLAND, G. & WEISS, I., 1958. – Die Kerngrösse triploider Krötenbastarde mit experimentell verdoppeltem mutterlichem Genom. *Zschr. mikrosk.-anat. Forsch.*, **64** : 129-158.

HOTZ, H., 1983. – *Genic diversity among water frog genomes inherited with and without recombination.* Thesis, Universität Zürich : i + 1-137.

MAYNARD SMITH, J., 1974. – Recombination and rate of evolution. *Genetics*, **78** : 299-304.

MULLER, H.J., 1932. – Some genetic aspects of sex. *Amer. Natur.*, **66** : 118-138.

OGIELSKA-NOWAK, M , 1985. – Stages of normal and spontaneous abnormal development of the natural hybrid *Rana esculenta* L. (Amphibia, Anura). *Zool. Polon.*, **32** : 37-62.

OHLER, A., 1987. – *Zur Ontogenie von* Rana *synkl.* esculenta. Thesis, Universitat Wien : 1-266.

SCHUBÖ, W. & UEHLINGER, H M , 1986. – *SPSSx Handbuch der Programmversion 2 2* Fischer, Stuttgart & New York : 1-659.

TRAVIS, J., 1981. – Control of larval growth variation in a population of *Pseudacris triseriata* (Anura, Hylidae). *Evolution*, **35** : 423-432.

TUNNER, H.G., 1973. – Demonstration of the hybrid origin of the common green frog *Rana esculenta* L. *Die Naturwissenschaften*, **60** : 481-482.

----- 1974. – Die klonale Struktur einer Wasserfroschpopulation. *Z. zool. Syst. Evolut.-forsch.*, **12** : 309-314.

----- 1979. – The inheritance of morphology and electrophoretic markers from homotypic crosses of the hybridogenetic *Rana esculenta*. *Mitt. Zool. Mus. Berlin*, **55** : 89-109.

----- 1980. – Kreuzungsexperimente mit Wasserfröschen aus österreichischen und polnischen Mischpopulationen (*Rana lessonae* + *Rana esculenta*). *Z. zool. syst. Evolut.- forsch.*, **18** : 257-297.

VOGEL, P. & CHEN, P.S., 1976. – Genetic control of LDH izosymes in the *Rana esculenta* complex. *Experientia*, **33** : 1285-1287.

WHITT, G.S., CHO, P.L. & CHILDERS, W.F., 1972. – Preferential inhibition of allelic isozyme synthesis in an interspecific sunfish hybrid. *J. exp. Zool.*, **179** : 271-282.

WIJNANDS, H.E.J., 1979. – Partial ecological isolation of *Rana lessonae* and *Rana esculenta* as a mechanism for maintenance of the hybrid form, *Rana esculenta* (Anura, Ranidae). *Mitt. Zool. Mus. Berlin*, **55** : 131-142.

WILBUR, H.M. & COLLINS, J.P., 1973. – Ecological aspects of amphibian metamorphosis. *Science*, **182** : 1305-1314.

WRIGHT, D.A. & MOYER, F.H., 1968. – Inheritance of frog lactate deshydrogenase patterns and the persistence of maternal isozymes during development. *J. exp. Zool.*, **167** : 197-206.


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